

***Pyrrhocoris apterus* (Heteroptera) – an experimental model species: A review**

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370 05 České Budějovice, Czech Republic**Development, reproduction, endocrinology, biochemistry, genetics, life history, behaviour, host plants, diapause, voltinism, wing polymorphism, parasites, Heteroptera, Pyrrhocoridae, *Pyrrhocoris apterus*, linden bug, red firebug**

Abstract. The red firebug, *Pyrrhocoris apterus* (L.), has been a convenient model for biological research for a long time. The interest in *P. apterus* increased especially with the discovery in the mid-1960's of the so-called "paper factor", i.e., a substance with juvenile hormone activity. Considerable research has been done on this model insect in research topics such as biogeography, embryology, developmental and reproductive biology, theoretical and applied endocrinology, biochemistry, cytogenetics and formal genetics, bionomics, ethology, pathology, voltinism, diapause, wing polymorphism, migration, pathogens, symbiotes and predators. Some of the newest studies are directed toward the problems of determination of metameric pattern, cold hardiness and biorhythms. Present review provides the first selective summary of data published in almost 300 papers.

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INTRODUCTION

The Pyrrhocoridae is a family of phytophagous land bugs (Heteroptera: Pentatomomorpha: Coreoidea s. lat.), including approximately 300 species, characterized by their general tendency to show warning colouration and by adaptation to host plants in the order Malvales (Slater, 1982; Ahmad & Schaefer, 1987; Zrzavý, 1990; Schaefer, 1993).

The distribution of the family is predominantly Palaetropical or subtropical-Palaearctic, but *Pyrrhocoris apterus* (L., 1758) is one of the few species extending to temperate zone of the Palaearctic Region and reaching eastwards to the south of western Siberia (up to the W. Altai Mts), SW Mongolia and NW China (Stichel, 1959; Kulik, 1973; Puchkov, 1974). *P. apterus* also has been found in the USA, Central America and India (Barber, 1911). Detailed geographic distribution of this species was reported by Stichel (1959) and Puchkov (1974).

Neither species-level taxonomy of *Pyrrhocoris*, nor phylogeny of the Pyrrhocoridae have been subjected to modern revision (Schaefer, 1993).

The red firebug, *P. apterus*, represents a widely distributed western Palaearctic species of the Pyrrhocoridae.

The importance of the red firebug, *Pyrrhocoris apterus*, as a convenient experimental tool for biological research seems to expand continually. Easy laboratory breeding is one of the main reasons of its wide use as a useful model species. The interest in *P. apterus* increased with the discovery in the mid-1960's of "paper factor", i.e., the substance with juvenile hormone activity (Sláma & Williams, 1965, 1966a,b). Earlier interest in this species appeared in 1891, when the German zoologist Herman Henking described chromatin elements from this bug, that he labeled X. This was, in fact, the first report on sex chromosomes in the history of genetic research. Since then, the morphology, physiology, endocrinology and genetics of *P. apterus* have been studied widely. However, in spite of the intensive basic biological research that has been accomplished with *P. apterus*, the available data obtained have not been reviewed extensively.

DEVELOPMENT

Eggs and embryogenesis

Newly laid eggs of *P. apterus* are ovoid in shape, white or off-white colour and characterized by the slightly excentric arrangement of micropylar ring (Southwood, 1956; Cobben, 1968). Their colour turns yellow-red, near the end of embryonic development (Rizki & Sláma, 1968; Smith & Forrest, 1969). The mean egg size of *P. apterus* decreases with female age (from the 1st to 6th batch) by an average of 16%; at low temperatures (18° and 19°C) the egg weight is decreased by 16–21% (Honěk, 1992). Decreasing egg size negatively affects the offspring quality (Honěk, 1986b, 1987b). Nearly 50% of the variation in body size in this species is determined by the size of the egg. Larvae hatching from small eggs are disadvantaged: cannibalistic contests are usually won by the larger of the combatants. Thus, the probability of survival of larvae from a large egg progeny is greater than that of larvae from small eggs (Honěk, 1992).

Normal eggs of *P. apterus* contain 4–12 aeromicropyles arranged in a ring at the anterior pole of the chorion (Hinton, 1981; Socha, 1988c); no micropyles are formed at the posterior pole (Cobben, 1968). The diameter of the anterior micropylar ring is approximately

60–70 μm , with each micropyle being 17 μm wide and 25 μm high. Each micropyle contains a canal approximately 4 μm in diameter (Mazzini, 1974). More than 6% of eggs laid by the *Apricot* (*Ap*) mutant of *P. apterus* represent abnormal “double micropyle ring” (DMR) eggs that have one micropyle ring at each pole of egg shell (Socha, 1988b,c). The DMR eggs, having an altered anteroposterior polarity in external chorion morphology, are the first eggs of this type reported for Heteroptera. Except for the extra micropyle ring, no other chorionic anomaly was observed in the DMR eggs. Reciprocal crosses between wild-type and *Ap* homozygous bugs demonstrated a maternal effect of the *Ap* mutation on the DMR egg production; nevertheless the DMR trait was not found to be primarily coded by the *Ap* gene (Socha, 1988c). In contrast to the *dicephalic* mutant of *Drosophila* (which has an altered pattern of egg shell polarity as well as an altered pattern of embryogenesis (Lohs-Schardin, 1982), most DMR eggs produce normally developing larvae of both sexes. The function and spatial distribution of cytoplasmic determinants, which are responsible for the normal course of oogenesis and embryonic patterning, were not disturbed by the appearance of the supernumerary micropyle ring in DMR eggs.

In the nature, the embryonic development lasts 10–14 days at 18–20°C (Tischler, 1959; Puchkov, 1974), but it can be prolonged on 24 days under lower temperature, or shortened on 6–8 days during warm and dry season of the year (Polozhencev & Polozhenceva-Korovina, 1961). In the laboratory, the embryonic development takes 7.5 days at 25°C (Matolín, 1973a). The threshold temperature for egg development is rather high, about 12°C (Honěk & Kocourek, 1990).

The morphology of embryonic development (egg, blastokinesis and eclosion) and gross characteristic of embryo was studied by several authors (Karavajev, 1894; Seidel, 1924; Cobben, 1968; Matolín, 1973a,b; Enslee & Riddiford, 1981) and found to be fairly typical of the Heteroptera in general, differing only in some details. Temporal sequences of the main stages in embryonal development can be summarized as follows (in hrs after oviposition at 25°C): meiosis (0–4); cleavage division (4–12); formation of blastoderm (16–19); differentiation and invagination of the germ band (24–48); segmentation of the embryo (60); differentiation of neuroblasts (65); rudiments of organ formation (70–72); blastokinesis (110–120); pigmentation (144) and hatching (168–180). References to older literature concerning mouthparts (including innervation of stylets) and putting these data into phylogenetic perspective can be found in Cobben (1978).

The *Pale* (*Pa*), *Ap* and *abnormal embryogenesis* (*ae*) mutations (Socha & Matolín, 1985; Socha, 1988a,b) are the only mutations known to disturb the embryogenesis of *P. apterus*. In contrast to pre-hatching and post-blastokinesis types of lethality observed in *Ap* and *Pa* mutants, the embryonic death caused by the sex-linked maternal effect of the *ae* mutation is due to disorders in the formation of germ bands in 54% of the cases. An average 93% lethality was found in eggs laid by *ae* homozygous females crossed with *ae/0* hemizygous males, in spite of their normal number and appearance (Socha & Matolín, 1985). Malformed embryos developed, with some structures deformed, reduced or lacking (Fig. 1). Abnormal larvae hatching from later batches of eggs laid by *ae/ae* females mated with wild-type males very much resemble the effects of the *almondex* mutation (*amx*, 1–27.7) of *D. melanogaster* (Shannon, 1972). However, some similar morphological abnormalities and teratologic effects also were observed occasionally among bugs from natural populations (Gadeau de Kerville, 1914; Balazuc, 1951).

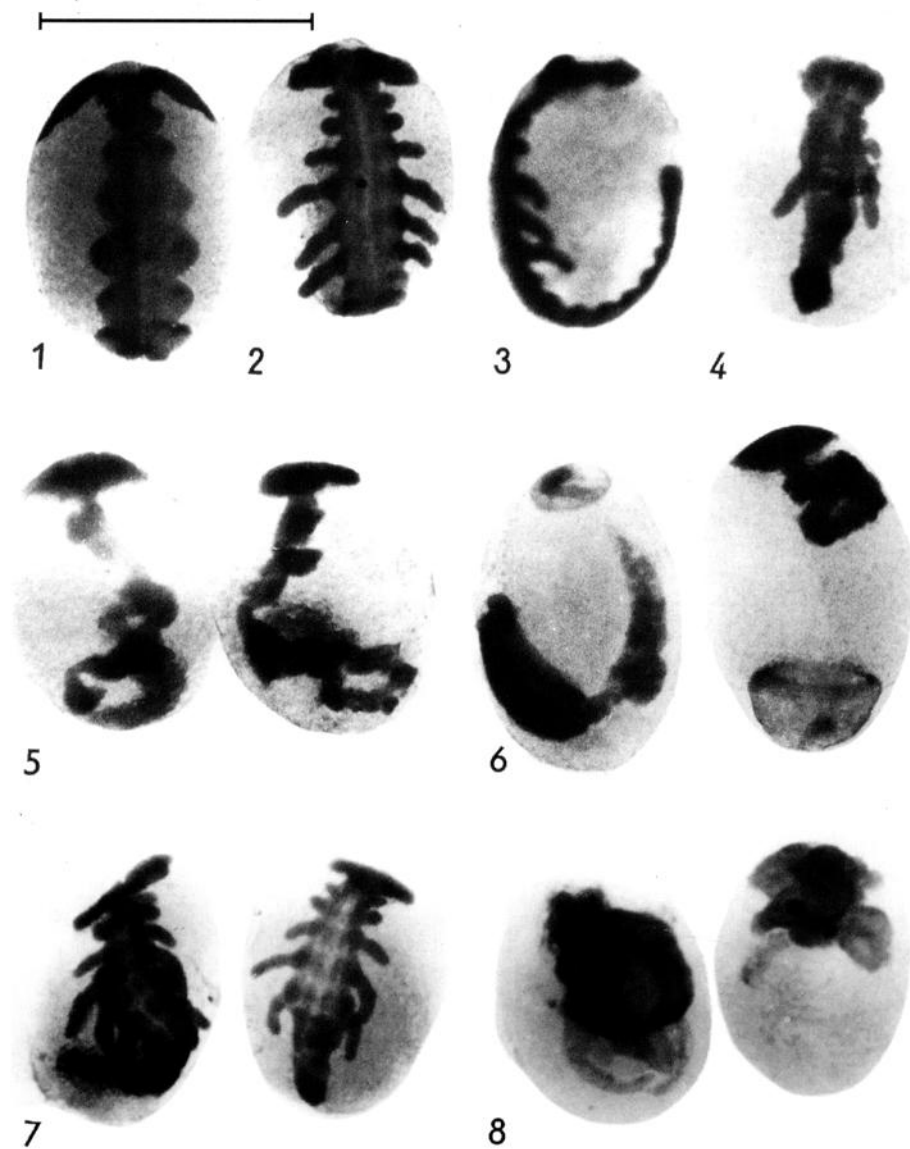


Fig. 1: Normal (wild-type) and disturbed (*ae* mutation) embryonic development in *P. apterus*. 1 – Normal development, segmentation of germ band (68 hrs); 2, 3 – Normal development and growth of appendages (72 hrs); 4, 5, 6 – Malformed germ band and abnormal segmentation (72 hrs); 7 – Normal (right) and asymmetrically deformed embryos (left) (72 hrs); 8 – deformed dwarf embryos (144 hrs). Carnoy, borax carmine, scale = 1 mm. From Socha & Matolín (1985).

Embryonic inviability reported for reciprocal crosses between allopatric species *P. apterus* and *P. sibiricus* could function as a major reproductive isolation barrier (Matolín & Štys, 1987).

The “Paper Factor” or juvenile hormone analogues (JHA) applied also induce a number of aberrations of embryogenesis that prevent hatching (Sláma & Williams, 1966a,b; Masner et al., 1968a,b; Matolín, 1970, 1971; Enslee & Riddiford, 1970, 1973, 1977). Development is inhibited frequently not only in functionally demanding processes (invagination of the germ band, blastokinesis) but even at the beginning of the blastoderm stage. When the development has been arrested at early stages, embryos do not die immediately but sometimes survive for quite a long time (Matolín, 1970). No differences were observed between the consequences of application to adults and eggs. The JHA-like defects in embryogenesis of *P. apterus* were observed also after treatment with chemosterilants (Matolín, 1973b).

Exposure of late embryos to juvenile hormone (JH) or JHA does not affect larval hatching, but results in delayed effects manifested 4 weeks later at metamorphosis (Riddiford, 1969, 1970, 1971, 1972). Riddiford & Truman (1972) interpreted this delayed action on metamorphosis by the ability of JHA to interfere with the programming of the embryonic corpora allata (CA). According to these authors the CA of the treated insects fail to stop secreting JH at the onset of the last larval instar (Riddiford & Truman, 1972). However, Socha with coauthors (Sláma & Socha, 1979; Socha & Hodková, 1981) showed this interpretation to be incorrect. Larval functions of the CA do not appear to be predetermined by exogenous applications of JHA in the late embryos, but, rather, the delayed effects are caused by the mere persistence of JHA from the late embryonic stage until metamorphosis.

Larval growth and metamorphosis

The larvae pass through 5 instars. Under constant laboratory conditions (long-day 18L : 6D and 26°C), the period including all initial four larval instars takes approximately 10–14 days, while the final instar lasts from 7 to 10 days (Rizki & Sláma, 1968; Socha, unpubl.). In nature, the duration of immature stages of the bug is considerably longer (Tischler, 1959), and it is controlled behaviourally on the basis of thermoregulation (Honěk & Šrámková, 1976). The larvae fail to develop at temperatures lower than 15°C (Honěk & Kocourek, 1990). It is probable that this is due to cessation of feeding activity at low temperatures (Honěk, unpubl.) Insect metamorphosis takes place when the CA cease to secrete JH. In *P. apterus*, the CA are inactivated in the late 4th larval instar (Hodková, 1978). The mechanisms engaged in the “counting of instars” reside in the neuroendocrine system of the brain. Apparently the brain is programmed already in the 3rd larval instar to inactivate the CA, but the inactivation occurs late in the 4th instar (Hodková, 1979).

In the selected genetic strain *reddish lobes* [*rl(17)*] of *P. apterus* (Socha, 1984), a few individuals go through metamorphosis precociously. The development of these 4th instar prothetelic adultiforms is characterized by the omission of the two last larval instars (Socha, 1987b). Abdomens of 4th instar prothetelic adultiforms display a characteristic black-red spotted pigmentation pattern, similar to that observed in larval-imaginal intermediates (adultoids) produced by allatectomy (Sláma, 1964a, 1965c). Two alternative explanations for this are possible: either the target tissue loses its sensitivity to JH or the CA

fail to produce JH during the 3rd larval instar. The latter alternative was supported by the finding that 4th instar prothetelic adultiforms did not ecdyse, apparently due to degeneration of their prothoracic glands (Socha, 1987b). Later experiments showed, however, that the production of 4th instar prothetelic adultiforms was the consequence of absence of the CA (Socha & Hodková, 1989). Since the individuals lacking their CA develop normally until the 3rd instar, the question arises whether this gland is essential for early larval development in this species. The conclusion that “the early larval system does not depend on JH” is supported also by observations that “antijvenile hormone agents usually become fully expressed only in the moult to fourth or fifth instar, irrespective of time of treatment” (Staal, 1986).

When the metamorphosis is inhibited partially by application of JHA, the intermediate forms display a variety of characters which are intermediate between two developmental stages (Carlisle et al., 1966; Williams & Sláma, 1966; Carlisle & Ellis, 1967; Socha & Hodková, 1981). The gross morphological effects of the treatments and the evaluation of the JHA effects on metamorphosis were described (Williams & Sláma, 1966; Sláma et al., 1974). The type and character of the intermediate forms were found to be dependent on two main factors: the time of application and the dose of juvenoid applied. In contrast to previous suggestions (Sláma et al., 1974), detailed microscopic examination of the cleaned cuticles of intermediate forms revealed the existence of composite cuticle, exhibiting larval morphological features combined with imaginal pigmentation (Willis et al., 1981). According to these authors the reprogramming of cuticular synthesis and secretion may be inhibited by JHA at two or more levels. However, the recent scanning electron microscope study (Sláma & Weyda, unpubl.) did not reveal any of intermediate cuticle forms observed by Willis et al. (1981). These results are rather in favour of the previous hypothesis that the action of JH is all-or-none at the level of a single cell (Sláma et al., 1974).

Differentiation of wings and abdominal segments

Differentiation of the wings in *P. apterus* is a complex process. During metamorphosis the melanins disappear from various areas of the larval wing lobes that were previously black, and the red pteridine epidermal pigment thus becomes apparent (Socha, 1984). Not only size and shape of the black spots on the adult forewing can vary but even their occurrence is not stable, both in normal and in reduced or irregularly aberrant wings (Henke, 1924; Seidenstücker, 1953; Socha et al., 1993). Changes in wing pigmentation, especially an extension and reduction of black wing colour pattern (melanization) have been studied in relation to natural or experimentally simulated environmental influences (temperature), geographical conditions, genetics, evolutionary trends, and some other factors (wounding, etc.) (Schulze, 1913, 1916; Henke, 1924; Meissner, 1928; Seidenstücker, 1953; Ulrich, 1953; Socha, 1984; Zrzavý, 1990; Zrzavý et al., 1993). Extremely melanic forms described as f. *sordida* Jakovlev and f. *carbonaria* Horváth were observed either in southern, warmer localities (e.g., Hungary) or during warmer years (Schulze, 1916; Seidenstücker, 1953). The form with partly extended black wing spots (f. *crassipuncta* Schulze) occurs mainly on northern localities of temperate zone. The long-time exposure to cold causes the black stripes on the wings (Henke, 1924; Seidenstücker, 1953). Extended melanization of the pronotum was also observed. The 18 local populations from Central Asia, Moldavia and Czech Republic were studied and pronotum of the bugs from western populations found to

be more melanized (Vinkler, 1975). An enormous reduction of wing length and changes in wing colour pattern can be induced by treatment with JH-like compounds (Sláma, 1962, 1964a).

The colour pattern of forewing can be modified both by reduction of the dark area (up to loss of all forewing spots) and extension of the dark area (up to fusion of both spots together, and of these fused spots with the posterior black margin of corium and/or with the black clavus). Some of the extreme forewing patterns can be selected for and fixed at least partially by genetic methods. Last instar larvae display twenty different wing lobe colour patterns (Socha, 1984). The prothetelic colour pattern which, to some extent, resembles the adult wing colour pattern, is very rare in a normal population but can be fixed as a genetic strain *rl(17)*. Thus, the appearance of the adult colour pattern is to a large extent "transposed" to the last larval instar (Socha, 1984, 1985). This trait is regulated by a polygenic inheritance system. Studies of environmental and endocrinological effects on the *rl(17)* strain show that expression of this trait is insensitive to both photoperiod and JHA treatment, and that the development of an adult-like colour pattern on wing lobes of the *rl(17)* strain occurs independently of the structural development of adult wings (Socha, 1984). Results from selection suggest that individual colour patterns can be selected independently (Socha, unpubl.). The possible developmental trends in wing lobe colour pattern in last instar larvae are pictured in Fig. 2.

Behaviour of epidermal cells during postembryonic development also has been studied (Zrzavý et al., 1993). Based on clonal analysis of pregenital abdominal epidermis of the *mosaic (mo)* mutant, the authors concluded that no cell clones exceed intersegmental

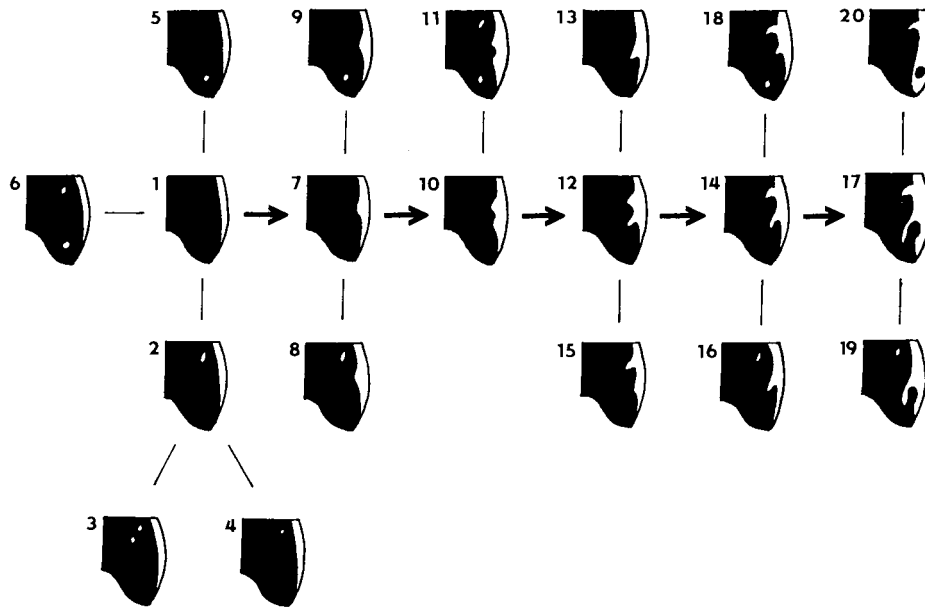


Fig. 2: Wing lobe colour pattern observed in the fifth instar larvae of the laboratory standard stock of *P. apterus* and during selection of the *rl(17)* strain. Wing lobe (No. 17) represents the type of colour pattern typical for the *rl(17)* strain.

boundaries. Whereas there are no absolutely insurmountable barriers within a segment, the border between anterior (red) and posterior (yellow) parts of segment's epidermis seems to be less exceedable for cell clones. These results are compatible with those obtained from *Oncopeltus fasciatus* (Dallas) (Heteroptera: Lygaeidae), as well as from other insects (including *Drosophila*), indicating that red and yellow epidermal bands are homologous to anterior and posterior compartments, respectively (Lawrence, 1973, 1981; Lawrence & Green, 1975; Campbell & Caveney, 1989; Zrzavý et al., 1993; Zrzavý & Štys, in prep.).

Morphological analysis of forewing colour-pattern formation and diversity in pyrrhocorids (Zrzavý, 1992) also suggests that the forewing is organized as a pair of compartments that are isolated from each other by a median fracture. This finding is highly compatible with the results obtained from *Drosophila* (Lawrence, 1991).

REPRODUCTION

Female reproductive system

The external morphology and internal anatomy of the female reproductive system and other organs were studied in relation to developmental stage (Mayer, 1874, 1875; Köhler, 1903; Seidel, 1924; Popovici & Dobreanu, 1941; Masner, 1966, 1968; Merle, 1969; Pluot, 1970; Sisli & Ayzev, 1979) or to comparative taxonomy (e.g., Carayon, 1950; Pendergrast, 1957; Scudder, 1959). Since the main topic of present review is focused on *P. apterus* as an experimental model species, the review does not include all comparative literature concerning the morphological and anatomical studies in relation to the classification of Heteroptera.

Adult females of *P. apterus* have a pair of telotrophic ovaries with 7 ovarioles in each ovary (Sláma et al., 1974). The ovaries of newly emerged adult females are relatively small, white or off-white, with a distinct lanceolate germarium and a vitellarium. Previtellogenic development is restricted to day 1, and it is followed by vitellogenic oocyte growth. In the majority of 2-day old females, 4–6 follicles can be distinguished in the vitellarium (Socha et al., 1988). The anatomical structure of an ovariole is schematized in Fig. 3. The oocytes are nourished by two nutritive systems: the trophocytes, which are already differentiated in newly emerged adults, and the follicular epithelium, which must first differentiate from the prefollicular syncytium (Masner, 1968). The transport of nutritive substances from the nurse cells to the oocytes was demonstrated by use of autoradiographic methods (Mays, 1972). The growing oocytes are enveloped by a unilayered follicular epithelium, and individual oocytes are separated by interfollicular plugs. The cells of the interfollicular plugs do not follow the same transformation sequence observed in the follicular cells. From day 4 the vitellaria of most females consist of two conspicuous parts. The distal part contains 5–6 follicles, almost as large as mature eggs, while follicles of the second ovarian cycle are beginning to differentiate in the proximal part (Socha et al., 1988). Choriogenesis and formation of the micropyle rings begins after completion of vitellogenesis (Köhler, 1903). The pre-oviposition period (expressed as the interval between adult ecdysis and first oviposition) of reproducing females reared under long-day photoperiod at 26°C is 6–10 days (Sláma, 1965c; Socha et al., 1988; Socha & Šula, 1992). After ovulation the empty follicles are shrunken and the corpus luteum, characterized by a broad structureless slightly-staining mass, is formed (Masner, 1968; Merle, 1969). Distinctly differentiated, medium-sized follicles of the second ovarian cycle can be found in

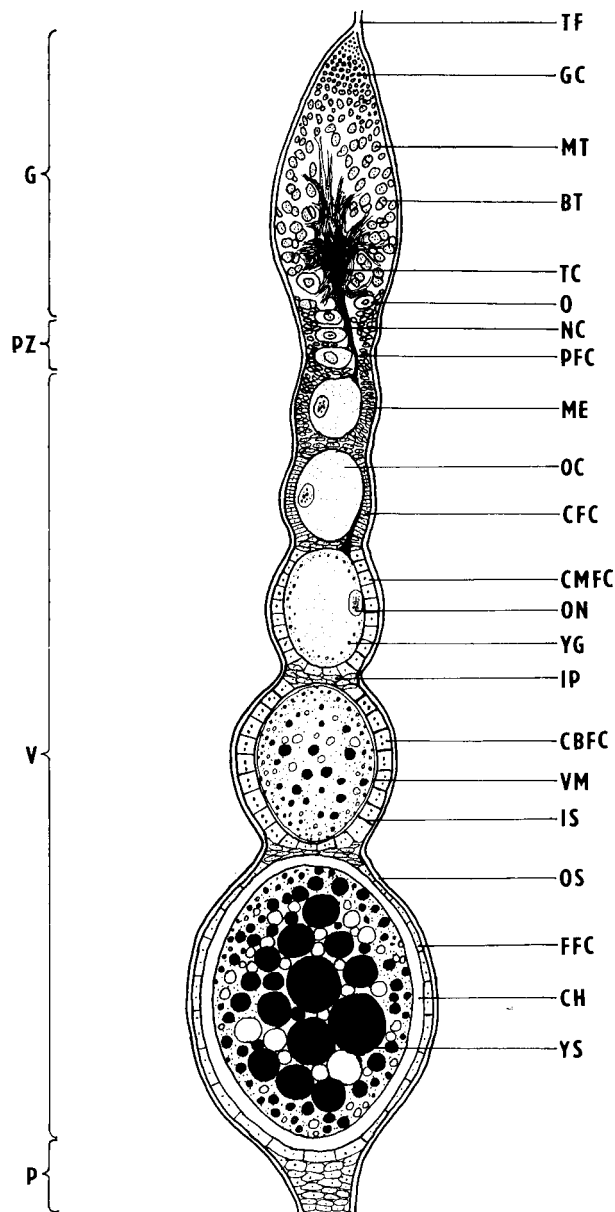


Fig. 3: Schematic diagram representing the longitudinal section of an ovariole in adult female of *P. apterus*. Explanation of symbols, BT – binucleate trophocyte, CBCF – cuboid binucleate follicular cell, CFC – columnar follicular cell, CH – chorion; CMFC – cuboid mononucleate follicular cell, FFC – flat follicular cell, G – germarium, GC – germal cell, IP – interfollicular plug, IS – interfollicular space, ME – multilayered epithelium, MT – mononucleate trophocyte, NC – nutritive cord, O – oocyte, OC – oocyte cytoplasm, ON – oocyte nucleus, OS – outer sheath, P – pedicel, PFC – prefollicular cell, PZ – prefollicular zone, TC – trophic core, TF – terminal filament, V – vitellarium, VM – vitelline membrane, YG – yolk granule, YS – yolk sphere. From Socha et al. (1988).

the proximal part of the vitellarium at this time. Further batches of eggs are mostly laid at intervals of 2–5 days (Sláma, 1971b; Sláma et al., 1974). About 50–80 oocytes develop simultaneously in each cycle, without any relation to insemination (Sláma, 1971b). The eggs are usually deposited all at once, the moment of oviposition separating individual cycles. The cycles may be prevented completely by cardiac-allatectomy and reinduced by implantation of a single corpus cardiacum-allatum complex taken from an active female (Sláma & Hrušková, 1963; Sláma, 1964a). The effect of photoperiod on the oviposition rhythms was studied in photoperiodically sensitive and non-sensitive females; preliminary data indicate that a component of circadian clock is related to photoperiodic determination of diapause (Hodková, 1988).

The effects of JH (Masner, 1966, 1968, 1969), JHAs (Sláma, 1965c; Masner et al., 1968a,b; Sláma et al., 1974), precocenes (Bowers et al., 1976; Hodková & Socha, 1982), chemosterilants (Landa, 1970; Masner, 1971; Masner & Landa, 1971; Gelbič & Šula, 1989, 1990), insecticides (Honěk & Novák, 1976, 1977), antiviral nucleoside analogues (Sláma et al., 1983; Votruba et al., 1985; Šula et al., 1987; Socha et al., 1988, 1989; Gelbič, 1992; Gelbič & Šula, 1992), photoperiod, temperature and population density (Hodek, 1968, 1971a,b; Honěk, 1983; Socha & Šula, 1992) on ovarian development and reproduction in *P. apterus* are well documented. Masner (1968) found that transformation of the follicular epithelium into a specialized secretory epithelium is induced by JH. In the absence of JH the follicular cells remain dormant, taking no active role in the transport of the material from the haemolymph to ooplasm. The gonadotropic effects of JHA were demonstrated experimentally (Masner, 1967, 1969). Allatectomized females treated with large doses of JHA started to produce and oviposit the eggs 5 days after treatment (Sláma, 1965c); diapausing females responded to JHA treatment in similar way. Without respect to the amount of reproductive cycles or number of eggs produced, the eggs deposited were sterile. Application of very active JHA on the females causes their permanent sterility (Masner et al., 1968a,b). Precocenes failed to inhibit ovarian development (Bowers et al., 1976; Hodková & Socha, 1982). The features of sterility and morphological aberrations of the ovaries, induced by antiviral nucleoside analogues (Sláma et al., 1983) and chemosterilants (Masner & Landa, 1971), are similar in many respects (e.g., all these compounds can affect directly dividing tissues and inhibit mitosis), but the mechanisms of their actions are different (Sláma et al., 1983; Gelbič & Šula, 1992). Scoring systems, distinguishing 4 to 6 stages of ovarian development (Hodek, 1968, 1971b; Saunders, 1983; Socha & Šula, 1992), were devised to classify ovarian states.

Male reproductive system

The morphology and anatomy of the male reproductive system were studied in relation to developmental stage (Ludwig, 1926; Merle, 1969; Ayzev & Sisli, 1979) or classification (Sing Pruthi, 1925; Pendergrast, 1957). The testes and different phases of spermatogenesis were studied, mainly, in connection with the pattern of chromosome distribution (Henking, 1891; Gross, 1907; Wilson, 1909a,b, 1912; Antropov & Bogdanov, 1970; Mess-thaler & Traut, 1975).

The testis is composed of 7 testicular tubules covered by a membrane. Each tubule is divided into an apical part and cysts, each of which contains groups of cells (spermatogonies, spermatocytes I and II, spermatids and spermatozooids) in the same

developmental stage (Merle, 1969). Two papers discuss ultrastructural details of spermatids (Godula, 1979) and spermatozoa (Furieri, 1965). Spermatids contain a unique basal body appendage that appears as a plaque, composed of four parallel, electron-dense lamellae (Godula, 1979). It is probable that the lamellar plaque serves as a rigid element providing a stable attachment for the microtubule organizing center and preventing its dislocation. The formation of the ordered microtubular arrangement in spermatids is mediated by a self-linkage mechanism. The total length of the spermatozoid is 950 μ (Furieri, 1965).

The relationship between the course of spermatogenesis and changes in the pattern of chromosome distribution are discussed under Cytogenetics.

Mating

The mating behaviour in both sexes is very simple; no special courting was observed. The male responds to the female by olfactory and other stimuli (Žďárek, 1968, 1970, 1971). Male mating activity appears on the 5th to 6th day after adult emergence. Sexually active females evidently produce a volatile substance which releases mating behaviour in the males. Female attractiveness and receptivity increase on the 4th day and attain maximum values by the 7th day after emergence. Copulation consists of three phases: 1. the male identifies the female from a short distance; 2. the male excites the female by contact stimulation after which he orients to a position from which copulation is possible; 3. when coupling is complete the pair assume an opposed position for the remainder of the copulation (Žďárek, 1971). Hellwig & Ludwig (1951), who studied mating behaviour in *P. apterus*, suggested that males first react to all moving buglike objects in their environment; when within short distance, however, only females of their own species stimulate the subsequent mating behaviour. Under laboratory conditions, the duration of copulation lasts from a few minutes to several hours (Žďárek, 1967). No significant differences were found between the mating or copulatory activity of normal active males and active males with blackened eyes; antennectomised males, however, showed very low levels of sexual activity (Žďárek, 1971).

Diapausing males did not copulate, but diapausing females in which diapause was artificially induced by short-day conditions at 25°C, were able to mate when paired with active males (in 16% of the cases, in comparison with active females). The attractiveness of these females was lower than that of active females, as was their receptivity (Žďárek, 1971). Both attractiveness and receptivity of the females were shown to be independent of the presence of JH. The gonads are not involved in control of mating behaviour in either sex, as is also true in other insect species (Žďárek, 1971). If copulatory activity under short-day conditions is taken as the criterion for termination of diapause in males, then males appear to be activated earlier than females (Hodek, 1971a). The presence of a reproductively active female has a much less important effect than photoperiod on the regulation of reproductive activity and diapause in the male (Hodková et al., 1991). The mating activity of males is determined directly by changes in the central nervous system induced by environment conditions terminating diapause. Many behavioural aspects of the diapause syndrome of adult diapause disappear after treatment with JHA (Sláma et al., 1974). Mating behaviour following termination of imaginal diapause, after allatectomy,

cardiacallatectomy and ovariectomy or after treatment with the products exhibiting JH activity has been studied thoroughly (Clementson, 1965; Žďárek, 1968, 1971).

Giant supernumerary larvae or adultoids induced by JHA exhibit adult sexual behaviour, an activity never observed in normal larvae (Žďárek & Sláma, 1968). The female supernumerary larvae are attractive to adult males and elicit mating behaviour. Male supernumerary larvae make efforts to copulate with adult females or with the female supernumerary larvae. Sexual behaviour in supernumerary larvae of both sexes is related to the degree of morphological and physiological effect of agents with JH activity (Sláma et al., 1974). Sexual activity may develop independently of the presence of external genitalia and the differentiation process of the gonads. Under certain circumstances sexual behaviour may develop despite the presence of active prothoracic glands, i.e., in the cases of supernumerary larvae which underwent a further moult (Žďárek & Sláma, 1968).

ENDOCRINOLOGY

Endocrines and hormones

Several schematic diagrams (Fig. 4) and photographs of the neuroendocrine complex of *P. apterus* are available (Novák, 1966; Hodková, 1976; Sláma et al., 1974; Socha & Hodková, 1989).

A cluster of 7 neurosecretory cells is located on the upper surface of each hemisphere of the brain, near the median furrow in the pars intercerebralis protocerebri (Novák, 1966). The neurosecretory cells in this region of the brain enable the bug to maintain water balance within certain limits (Gutmann & Novák, unpubl., in Novák, 1966). The roles of the nervi allati and centres of the pars intercerebralis in the regulation of the secretory activity of the CA was studied under long- and short-day photoperiodic regimes. Extirpation of the pars intercerebralis resulted in low reproductive activity regardless of the photoperiod used. The pars intercerebralis appears to contain both stimulatory and inhibitory centres (Hodková, 1976).

The role of activation hormone in metabolism of *P. apterus* was studied by several authors (Sláma, 1964a, 1965a, 1971b; Sláma & Žďárek, 1974; Janda & Sláma, 1965; Němec, 1981). They demonstrated that an extirpation of corpora cardiaca influences the carbohydrate, lipid and protein metabolism. The activation hormone has a stimulatory effect on oxygen consumption (Sláma, 1965b) and secretions of various glandular tissue (Němec et al., 1967; Nohel & Sláma, 1972; Sláma et al., 1974). The most affected tissues after removal of the corpora cardiaca (which inhibits completely the activation hormone release in the bug) are "trophic" tissues. It is most probable that the role of activation hormone in the reproductive cycle depends upon its regulation of the nutritive functions of the organism, through stimulating growth and metabolic activities in tissues engaged with digestion and food utilisation (Sláma, 1971b). The effects of injury of endocrine organs in *P. apterus* were described also by some other authors (Maslennikova & Chernysh, 1979).

A possible role of melatonin in transmission of photoperiodic signals and in photoperiodic regulation of reproduction in *P. apterus* has been recently suggested (Hodková, 1989, 1990). The photoperiodic information governing the diapause or non-diapause developmental programme, which is manifested by different levels of inhibition of CA, is maintained within the transplanted neuroendocrine system irrespective of the photoperiodic conditions of recipients (Hodková, 1992).

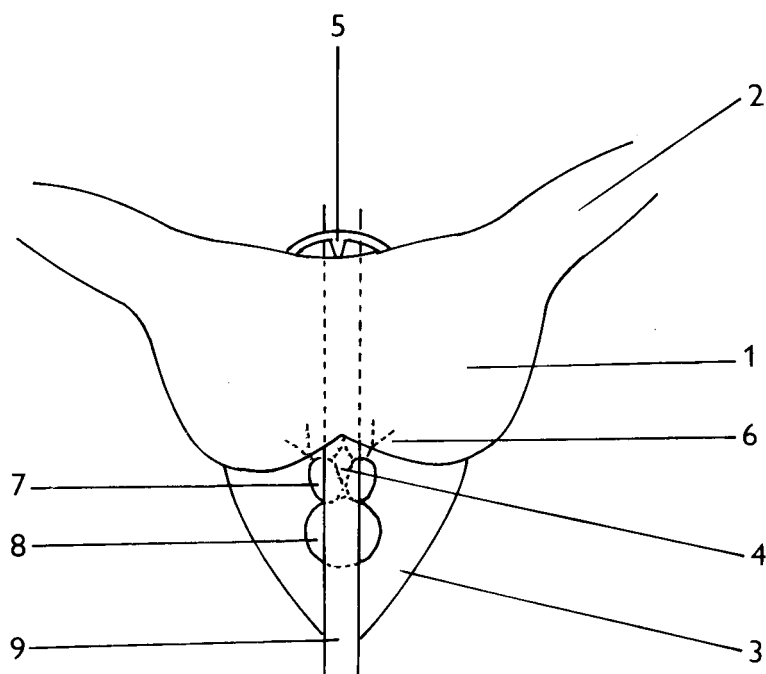


Fig. 4: Schematic diagram of the neuroendocrine complex of *P. apterus*. 1 – protocerebrum; 2 – optic lobes; 3 – suboesophageal ganglion; 4 – hypocerebral ganglion; 5 – frontal ganglion; 6 – nervi corporis cardiaci; 7 – corpora cardiaca; 8 – corpus allatum; 9 – aorta. From Socha & Hodková (1989).

A fused, single CA is the typical form of this gland in *P. apterus* (Novák, 1966). However, abnormalities due to incomplete fusion of the original paired rudiments towards the end of embryonic period (sometimes even showing two separate bodies) were often found (Novák, 1956, unpubl.). Studies on the activity pattern of the CA during larval development showed that the gland is inactivated during the second half of the 4th instar (Hodková, 1978) and is again reactivated several days after ecdysis to the 5th instar (Novák & Červenková, 1959). The mechanisms involved in the regulation of the CA in both larvae and adults are known. The reactivation of the CA during metamorphosis is associated with a change in dependence on the brain. While the activity of larval CA is maintained by stimulation from the brain (Hodková, 1978, 1979), the adult CA becomes relatively independent of brain stimulation and can be activated by removing the nervous inhibition (Hodková, 1976, 1977c).

The possibility of a quantitative test for CA activity based on its metabolic effects has been suggested by Sláma & Hrušešová (1963). The implantation of an active gland into an allatectomized adult female causes a specific increase in the oxygen consumption of the recipient. This increase appears to be directly proportional to the activity of the gland. The effect of an implanted CA on that of the recipient was studied using a biometrical analysis of gland volumes (Novák, 1966). The size and gonadotropic activity of the CA after different surgical treatments were studied in detail. Although there may be a correlation

between the CA volume and its activity in intact females, no such correlation was found after surgical interventions (Hodková, 1977b).

In contrast to the results obtained by Riddiford & Truman (1972), no delayed effect of the application of JHA to mature embryos on the activity of CA in the penultimate and the last instar larvae was observed (Socha & Hodková, 1981). The application of JHA neither decreases the activity of CA when the CA remains naturally active (in the course of the 3rd instar) nor prevents inactivation of the CA during the penultimate instar. Neither negative nor positive feedback between JHA and CA in two larval instars preceeding the last larval instar was observed (Hodková & Socha, 1987). However, the application of JHA prevented the reactivation of the CA which occurs naturally during the last larval instar. Thus, CA of superlarvae were as inactive as the CA of normal larvae at the onset of the last larval instar. There was a negative feedback between JHA and CA in the last larval instar. The inhibitory effect of JHA on reactivation of the CA during metamorphosis may not be the result of a simple negative feedback observed in the adult insect but the result of an inhibition of "metamorphosis" of the brain and/or CA (Hodková & Socha, 1987). Allatectomy suppresses ovarian development and induces deep changes in the metabolism of glycogen, lipid, proteins and respiration (Sláma & Hruběšová, 1963; Sláma, 1964a,b, 1965b,c; Janda & Sláma, 1965).

There have been very few studies on prothoracic gland hormone (PGH) of *P. apterus*. Removal of prothoracic glands (PG) from larvae of the bug does not inhibit digestive metabolism but, after prolonged periods during which ecdysis does not occur, there is a continuous decrease in respiratory rate due to hypertrophy of the body and inability for larval instars to continue growing beyond certain limits (Sláma et al., 1974). The last instar larvae with the removed PG are able to feed, and perform all main physiological functions with exception that they cannot moult. Moulting deficiencies, toxic and antisclerotization effect on larvae can be induced by application of some sterol and androstane derivatives (Hora et al., 1967; Lábler et al., 1968; Velgová et al., 1969). The role of the PGH in the last larval instar may be in some physiological respects similar to that of JH in adult females (Sláma et al., 1974). Determination for breakdown of the PG proceeds at very beginning of metamorphosis just after the ecdysis into the last larval instar. Therefore, implantations of CA performed later resulted in formation of adultoids which were unable to undergo additional moult cycles (Sláma et al., 1974). An inhibitory action of ecdysterone on ecdysis or oviposition in females was found, when applied after the culmination of the endogenous ecdysteroid peak (Sláma, 1980). Injected ^3H -ecdysone was reversibly bound to one of the electrophoretically separated haemolymph proteins (Emmerich, 1970). There were found to be more kinds of binding sites and different association constants for these complexes. The ^3H -ecdysone can be metabolized in the tissues, but not in the haemolymph (Emmerich, 1970). Emmerich assumed a presence of some temperature dependent system which might be involved in transport of ecdysone from cytoplasm to nuclei.

In spite of the above findings, makisterone A was reported to be a true moulting hormone in *P. apterus* (Zachardová et al., 1989). The body content of makisterone A was correlated with the diapause and gonadal development during metamorphosis. These data indicate that a high titre of this hormone in diapausing adults prevents initiation of vitellogenesis, possibly by suppressing the rise of JH.

Hormonal analogues

In 1965 Sláma & Williams discovered that certain American paper products contain a source of a high JH activity for *P. apterus*. The active principle, called “paper factor”, was found to have its origin in the wood of certain pulp trees, especially that of the balsam fir, *Abies balsamea*. It exhibited perfect JH activity on *P. apterus*, but was inactive completely on other insects tested (Sláma & Williams, 1965, 1966a,b). The active principle was identified as a methyl ester of the known todomatuic acid, then called juvabione. A number of different substances with JHA activity were isolated from plants (Sláma, 1969). The first aromatic JHA were related structurally to juvabione (Sláma et al., 1968) and acted on pyrrhocorids exclusively. One of the most active isoprenoid compounds with JH activity for *P. apterus* is an ester of 3,7,11-trimethyl-7,11-dichloro-2-dodecenic acid (Romaňuk et al., 1967). Based on certain similarities between terpenic and peptidic chains, a new form of juvenoids – peptides (Poduška et al., 1971), for example L-isoleucyl-L-alanyl-p-aminobenzoic acid ester, with a high activity on *P. apterus* were prepared (Zaoral & Sláma, 1970). Like the juvabione-type compounds they are active on pyrrhocorids only. Other non-terpenic compounds also exhibited JH activity in *P. apterus* (Sláma, 1962). The idea of using the JHA as potential pesticides came into general consideration mainly in connection with the discovery of “paper factor” (Sláma & Williams, 1965, 1966a,b; Williams & Sláma, 1966) and chlorinated isoprenoids with potent contact action (Romaňuk et al., 1967; Masner et al., 1968a,b; Sláma et al., 1968). A great number of natural and synthetic materials with JH activity on *P. apterus* were described and tested (Sláma, 1971a; Sláma et al., 1969, 1974). The effects of JH and various JHA on embryogenesis, growth, metamorphosis, reproduction, behaviour, metabolism and several physiological and biochemical parameters of *P. apterus* can be found in particular sections of the present paper.

Compounds with “anti-JH activity” were considered to be potentially more useful against the harmful, feeding, immature stages of pest insects than JHA (Staal, 1986). Precocene I (P I) and precocene II (P II) were the first compounds reported to possess such activity in insects (Bowers et al., 1976) and regarded as a prototype of fourth-generation insecticides. In contrast to *O. fasciatus* and *Dysdercus cingulatus* (F.), *P. apterus* is known to be insensitive to the anti-allatotrophic agent precocene II (Bowers et al., 1976; Hodková & Socha, 1982). The failure of P II to inhibit ovarian development in *P. apterus* appears to be caused by both a low sensitivity to P II of the CA itself and some unknown specific mechanisms outside the CA (Hodková & Socha, 1982). Sláma (1978) suggested that it was probable that inhibitory effects of precocenes observed in vivo are due to their anti-feedant property, and need not be specifically antihormonal. In a later study, however, at least three kinds of effects, antifeedant, lethal and allatotoxic, were recognized (Socha & Hodková, 1983). The in vivo allatotoxic effect of P II was proved to be direct, being mediated neither through nerve connection of the CA with the brain (Hodková & Socha, 1982) nor by antifeedant effect of this agent (Socha & Hodková, 1983).

BIOCHEMISTRY

Nucleic acids

DNA content in the ovaries and fat body increases during the first reproductive cycle, but the increase in the fat body is less conspicuous and ceases towards the end of the cycle

(Forejtová & Čermáková, 1973). According to other authors (Mácha, 1969), only the RNA content increases during oogenesis, while the DNA content remains unchanged. The transfer of DNA from the fat body into ovaries has not been proven. ^3H -thymidine is incorporated during previtellogenesis in the DNA of follicular and nutritive cells, and during vitellogenesis also into the cytoplasm of oocytes (Forejtová & Čermáková, 1973).

The content of nucleic acids in some organs of adult *P. apterus* females was shown to be affected by JH (Hodková, 1974). In contrast to ovaries and fat body, no significant alteration in RNA or DNA content was observed in the midgut. Thus, JH seems to have no influence on nucleic acid content in this tissue during the reproductive cycle.

Proteins and enzymes

The haemolymph protein concentration is relatively low (about 30 mg/ml) at the beginning of both the 4th and 5th larval instars and then increases (Brettschneiderová, 1966). The increase at the beginning of each instar correlates with the most intensive feeding period.

Cyclic quantitative changes in protein concentration in adult females were studied by Sláma (1964b). He observed very large increase of proteins in the haemolymph of both allatectomized and ovariectomized *P. apterus* females and concluded that the protein accumulation was not associated directly with allatectomy. According to Sláma (1964b) the hormones regulate haemolymph protein concentration indirectly only. However, his conclusion appears to be true only in the case of ovariectomized females; in their haemolymph the vitellogenin accumulates in response to secretory activity of the CA. With regard to the accumulation of proteins in allatectomized females and protein regulation by JH, Sláma's conclusions are incorrect. It was shown clearly (Socha et al., 1991) that, in contrast to ovariectomy which increases the vitellogenin titre, other proteins accumulate after allatectomy. In allatectomized animals, vitellogenin was lacking completely. Proteins accumulating in the haemolymph of allatectomized females and diapausing adults appear identical (Socha et al., 1991; Socha & Šula, 1992). They may belong to a large group of storage proteins, so-called methionine-rich proteins, which are known to be suppressed by JH but induced by allatectomy (Kanost et al., 1990). This is corroborated by the fact that the storage proteins predominate in the haemolymph of diapausing adults (Socha & Šula, 1992) whose CA are inactive. Thus, the accumulation of these proteins in the haemolymph is due to the absence of JH rather than the inhibition of the growth of ovaries.

A vitellogenic female-specific protein ($R_m = 0.14$) was demonstrated in egg yolk and female haemolymph of *P. apterus* by native PAGE. SDS-PAGE revealed two subunits of the female-specific protein with M_r 186 and 150 kDa (Socha et al., 1991). The temporal pattern of female-specific proteins revealed a clear correlation with oocyte development. During the first gonadotropic cycle both the 150 and 186 kDa polypeptides were not detected in previtellogenic females. The first traces of these polypeptides appeared on day 2, after adult ecdysis, and their maximal titres were recorded on day 4. From that age their titres dropped. Nevertheless, vitellogenin could still be seen at the end of the first gonadotropic cycle. In the fat body the time course was similar, and the maximal titre of vitellogenin was noted on days 4 and 6. The 150 kDa polypeptide was found also in the yolk. Since its reaction to the anti-vitellogenin antiserum was positive, it was identified as vitellin (Socha & Šula, 1992). As its titre is not high in the yolk, it seems likely that vitellin

undergoes proteolysis in the yolk of eggs, prior to laying, and that, at least, some polypeptides occurring in the yolk are products of this lysis. In addition to the 150 kDa polypeptide, the yolk contains many other proteins that bind to anti-vitellogenin and that were also found in ovaries. Most of them had no counterparts in our samples of the haemolymph from vitellogenic females. The identification of the 150 kDa polypeptide as vitellogenin was accomplished by means of ovariectomy and immunoblotting (Socha et al., 1991). Allatectomy of the females resulted in vitellogenin disappearance and a rise in 78 and 82 kDa polypeptides in the haemolymph. Application of a JHA restored the ability of allatectomized females to produce female-specific polypeptides and to sequester them into the ovaries. Thus, the synthesis of the 186 and 150 kDa polypeptides is JH-dependent (Socha et al., 1991; Gelbič et al., 1992). The JH-dependent regulation of vitellogenin synthesis and the reasons for protein accumulation in the haemolymph of allatectomized *P. apterus* females do not confirm Sláma's (1964b) and Emmerich's (1970) conclusions. Despite a sensitive immunological method, the results of Socha & Šula (1992) did not confirm the presence of vitellogenin either in the haemolymph of last instar larvae or adult males as reported by Emmerich (1970). The bands observed by Emmerich were actually mixtures of proteins of similar mobility, because his technique employed separation methods that did not allow high resolution.

The activity of enzymes in various tissues of *P. apterus* was studied in relation to morphological stages or to the effects of hormones (Němec et al., 1969; Němec, 1972). Esterase activity in the intestine and Malpighian tubules increases cyclically at the beginning of each reproductive cycle, in connection with hormonally stimulated growth and metabolic changes. The haemolymph esterase activity showed the opposite pattern (Němec et al., 1969). Esterase activity was demonstrated also for some of electrophoretically separated haemolymph proteins in both the larvae and adult bugs (Emmerich, 1970). It appears that JHA affects esterase activity only indirectly, by controlling morphogenetic processes (Němec, 1972). The most active transaminase enzyme in the bug appears to be glutamate-pyruvate transaminase (Nohel & Sláma, 1972). The enzyme activity is inversely proportional to the total metabolic rate and is controlled neither by JH nor any other known hormone of the neuro-endocrine system. The effect of hormones on intestinal proteinase activity was studied in adult bugs (Hrubešová & Sláma, 1967). The intestinal and excretory phosphatases of the adults were reported to be inhibited by open-chain nucleoside analogues (Němec & Sláma, 1989; Gelbič & Šula, 1992). The activity of phosphatases was studied also in the *mo* mutant of *P. apterus*, a mutant characterized by pteridine accumulation in Malpighian tubules (Socha, 1987a). The activities of both acid and alkaline phosphatases decreased with age in both *mo* and wild-type adult males. However, adult *mo* males exhibited significantly higher activity of these enzymes than the wild-types, thus indicating some abnormalities in the function of the excretory organs (Němec & Socha, 1988).

Glycids, lipids and other nutrients

Changes in saccharides, lipids, nitrogen (Maciucă, 1934, 1935; Janda & Sláma, 1965; Janda, 1968, 1969; Stadler-Martin, 1969a,b; Sláma, 1971b; Divakar & Němec, 1973; Němec, 1977, 1981), and oxygen consumption (Sláma, 1960, 1964d, 1965a,b, 1969;

Novák & Sláma, 1962), were determined for various postembryonic stages in both control or hormonally-treated specimens.

In the first 2–3 days of reproduction cycle the body weight increased from 50 to 80 mg and the total body dry matter content was almost doubled. This is connected with restricted feeding in the second part of the reproductive cycle. A single batch of eggs may represent more than one third of the total dry matter of the body. Thus a considerable amount of energy rich substances has to be rebuilt by the metabolic machinery of the females in each cycle (Janda & Sláma, 1965). The initial feeding period is associated with an almost two fold increase of the fat body and protein bound nitrogen (Janda & Sláma, 1965).

The saccharide content and lipid composition in various organs were studied in relation to maturation of oocytes. The glycogen content in ovaries increases progressively during the reproductive cycle but, in other organs, glycogen accumulates only during the first half of the cycle (Němec, 1977). After allatectomy, an enormous amount of glycogen accumulates, mainly in the fat body; in contrast, ovariectomy induces the accumulation of lipids in the fat body (Němec, 1981). It is most probable that the conversion of carbohydrate into lipid was stimulated by the action of JH.

P. apterus is similar to other insects in having a triglyceride as the predominant class of lipids in the fat body but is distinctive in having an unusually high (more than 50%) proportion of linoleate among its fatty acids, presumably owing to its diet (Stadler-Martin, 1969a,b). During the first 5 days after larval-adult ecdysis the fat body first accumulates lipid and then releases it for utilization by the ovary. This storage of lipid in the fat body represents an important adaptation since it frees the insect from dependence on a constant food supply during vitellogenesis.

Growth and oxygen consumption rates increase at the beginning but decrease towards the end of each larval instar in *P. apterus* (Sláma, 1960). Similar cycles of growth and respiration in connection with cycles of reproduction and oviposition were found also in adult females (Sláma, 1964a). It has been demonstrated that the U-shaped metabolic curves, which occur normally in the last larval instar, may experimentally be induced in the foregoing larval instar by induction of metamorphosis. However they disappear from the last larval instar if the metamorphosis is delayed. According to Sláma (1964a,b,d, 1965a,b), the hormones control the total body metabolism indirectly by stimulating the growth processes in special “target” cells or tissues. Under the presence of the particular hormone the appropriate “target” organs begin to perform their physiological functions, which results in an increased metabolic activity (Sláma & Hruběšová, 1963; Sláma, 1964a,b,c,d; Janda & Sláma, 1965).

Pigments

The Pyrrhocoridae are large, robust insects with bright colouration. The colour polymorphism in *P. apterus* is due to variation in the content of various pigments, mainly melanins and pterins. Melanin represents the basic pigment, responsible for cuticular colouration. Its amount is increased considerably in melanized forms (Schulze, 1918; Henke, 1924; Seidenstücker, 1953) and in the *melanotic* mutant of *P. apterus* (Socha, 1984). Pteridines are deposited mainly in epidermal cells, but also in Malpighian tubules and other structures. Pteridine content in wild-type adult bugs and their eggs were studied

by several authors (Merlini & Mondelli, 1962; Merlini & Nasini, 1966; Smith & Forrest, 1969). Using paper or thin-layer chromatography they found erythropterin, isoxanthopter-in, violapterin and 7-methylxanthopter-in in the adults, and one more pterin, identified as 6-substitued derivate of violapterin, in the developing eggs. Both the number and concentration of pteridines increase as embryogenesis progresses. The egg colour becomes red at the end of embryonal development, due mainly to accumulation of erythropterin and isoxanthopter-in (Smith & Forrest, 1969; Socha & Němec, 1992). Recently, three more violapterins and also three xanthopterins of a distinct Rf and fluorescence were reported for the adult bugs of this species (Socha & Němec, 1992). The collection of various colour mutants of *P. apterus* (see section Formal genetics) allows detailed investigation of genetic aspects of pteridines synthesis and distribution (Socha & Němec, 1992). The *mo* mutant is the richest in both the number of pteridines concentration; the poorest is *Pa* mutant. Two groups of traits could be distinguished with regard to the pteridine distribution in the organs studied. The first group involving the wild-type, *mo* and *Ap* mutants, was characterized by the presence of erythropterin but the absence of xanthopter-in and leucopter-in in the integument and haemolymph. The second group with *white* (*wh*) and *yellow* mutants was characterized by the presence of xanthopter-in I and, in the case of *wh* mutant also leucopter-in, but by low content or absence of erythropterin. The *Pa* mutation could be considered a special case of the first group (Socha & Němec, 1992).

GENETICS

Cytogenetics

Cytologically, the Pyrrhocoridae are a heterogenous group. Eight genera and 16 species have been investigated cytologically. Chromosome numbers range from 13(12 + X₀) to 33(32 + X₀), with some multiple X_nO systems; all multiple sex chromosome systems found in Heteroptera appear to originate by fragmentation (Ueshima, 1979).

Cytological studies on *P. apterus* were undertaken by the German zoologist Hermann Henking (1891), who first reported the existence of the sex chromosome not only in this genus, but also for all of the animal kingdom. The X-chromosomes are nearly twice as large as any of the other chromosomes (Wilson, 1909a,b). The chromosomes of heteropterans, including *P. apterus*, are holocentric and have no localized or individualized centromere. The diploid number of chromosomes in *P. apterus* is $2n = 24$ in females and $2n = 23$ in males (Henking, 1891; Ueshima, 1979); the bug thus belongs to the XO-type of sex determination. However, exceptionally, males with supernumerary X-chromosomes ($n = 11A + X_1X_2O$) were also found in this species (Gross, 1907).

In addition to the small diffuse chromocentres, there is no distinct heterochromatin body in either female or male somatic tissues. Heterochromatization of sex chromosomes in *P. apterus* was reported for cells undergoing spermatogenesis (Henking, 1891; Wilson, 1909a, 1912). Primary spermatogonia are free of a heterochromatic body as are the secondary spermatogonia, up to the stage of 32 cell cysts. From 64 cell cysts onwards through to the meiotic prophase one heteropycnotic body is present which is inactive transcriptionally (Messthaler & Traut, 1975). Wilson (1909a) was able to trace this chromosomal element, which had been detected by him and Henking (1891), to the univalent X-chromosome of the last spermatogonial division. This element is distributed in only one of the two daughter nuclei in anaphase II, thus giving rise to spermatids with and without

X-chromosome which is still heterochromatic. The cytology of chromosomal configuration in the course of meiosis in relation to the cytophotometry of DNA and histones in the spermatids was studied by Antropov & Bogdanov (1970).

In addition to inactivation during spermatogenesis, the X-chromosomes are heterochromatic and inactive transcriptionally during an early phase of oogenesis (Messthaler & Traut, 1975). While the ovarioles of the 3rd and 4th instar larvae do not contain nuclei with prominent heterochromatic bodies, a deep-staining heterochromatic body becomes visible in the 5th instar larvae, in the early pachytene stage. Whether or not the X-chromosomes regain activity before the chromosome complement is inactivated in later stages of oogenesis, could not be detected (Messthaler & Traut, 1975).

Formal genetics

Following the discovery of sex chromosomes, *P. apterus* was forgotten virtually by geneticists. The formal genetics of this species was not investigated until 1968, when the *wh* body colour mutant was described (Rizki & Sláma, 1968). This trait, characterized by the inhibition of biosynthesis of the red pigment, was shown to be inherited as a single autosomal recessive trait. The occurrence of a female mosaic for the mutant trait and normal pigmentation indicates that white integument is autonomous and the presence of red pigment in other cells of the same individual will not supplement the colour deficiency (Rizki & Sláma, 1968).

Later, the following mutations and strains of *P. apterus* were described and analyzed: *yellow* (*yw*) (Socha, 1984); *melanotic* (*m*) (Socha, 1984, 1985); *mosaic* (*mo*) (Socha, 1987a); *Pale* (*Pa*) (Socha, 1988a); *Apricot* (*Ap*) (Socha, 1988b); *abnormal embryogenesis* (*ae*) (Socha & Matolín, 1985); *macropterous* (*ma*) (Honěk, 1986a); *unstable micropterous* (*ump*) (Socha et al., 1993); *non-diapause* (*nd*) (Hodková & Socha, 1992); *reddish lobes* [*rl*(17)] (Socha, 1984, 1985) and *yolk body* (*yb*) (Socha, unpubl.).

The above mentioned traits include mutations or strains which affect egg chorion formation (Socha, 1988b,c), embryogenesis (Socha & Matolín, 1985), wing length (Honěk, 1986a; Socha et al., 1993), pigmentation (melanine or pteridine pigments) (Rizki & Sláma, 1968; Socha, 1984, 1987a, 1988a,b), diapause induction (Hodková & Socha, 1992), and the course of metamorphosis (Socha, 1984, 1987b). Seven mutants (*wh*, *yw*, *yb*, *m*, *ma*, *nd*, *ump*) are inherited as autosomal recessives, two (*Pa*, *Ap*) as autosomal dominant and three (*ae*, *mo*, *ump*) are sex-linked recessives. Two mutations (*mo* and *ump*), that exhibit a genetically unstable nature are possibly transposon-mediated (Socha, 1987a; Socha et al., 1993). Two mutations (*ae* and *Ap*) exhibit a clear maternal effect: the first is embryonic lethal and the second affects formation of the micropyle ring.

LIFE HISTORY AND BEHAVIOUR

Bionomics

Pouvreau (1963) and Schlagbauer (1966) list papers devoted to *P. apterus* biology. Although Pouvreau dealt with some aspects of diapause, he did not attempt a full analysis of inducing and terminating factors, and Schlagbauer restricted himself to studying the food of the bug and to achieving a continuous breeding of four generations. There are other papers discussing various aspects of rearing methods and biology of the bug (Meissner, 1928; Schulze, 1918; Herold, 1922; Klein-Krautheim, 1936; Wagner, 1939; Mitrovic,

1949; Ulrich, 1953; Schwoerbel, 1956; Tischler, 1959; Marié, 1960; Puchkov, 1974; Pluot, 1978). The paper of Puchkov (1974) is particularly important since, with the exception of taxonomy and distribution, it contains much information on the ontogeny, ecology and host plants of *P. apterus*, and also includes a lot of special references on bionomics of this species.

In the field (Central Europe), the life cycle (period from the egg to adult emergence) takes about 2–3 months (Tischler, 1959; Puchkov, 1974). In the laboratory, i.e., at temperatures of 25–26°C and long-day (18L : 6D) photoperiod, this developmental period lasts about 1 month. Under laboratory conditions hatching occurs about 7–10 days after oviposition (Rizki & Sláma, 1968; Matolín, 1973a; Socha & Matolín, 1985). The rate of larval development at 25°C is relatively rapid at both short (< 14.5 hr per 24 hrs) and long (> 16.5 hr per 24 hrs) photoperiods, but is protracted significantly at intermediate or “critical” daylengths (Saunders, 1983).

The sexes of adults, and even of the penultimate (4th) and the last (5th) instar larvae, are easy to distinguish. Since the sexing larvae is an easy way to obtain virgin adult females, this method is advantageous, particularly for genetic crosses (Rizki & Sláma, 1968). Body length in adults, from natural populations, varies between 6.5–12 mm, being 6.5–11 mm in males and 7–12 mm in females (Puchkov, 1974; Honěk, 1981). The body size of adults is influenced mainly by the egg size, but modified substantially by temperature and food quantity and quality (Honěk, 1986b, 1987b). Body size, fecundity and the length of the life cycle are very sensitive to environmental factors, particularly temperature, nutrition and humidity, depend on population density (Hodek, 1968; Honěk, 1983), and differ somewhat among the various populations, strains and mutants (Meissner, 1928; Herold, 1922; Henke, 1924; Seidel, 1924; Schwoerbel, 1956; Tischler, 1959; Puchkov, 1974; Honěk, 1986b, 1987b, 1992; Socha, 1988a,b). Size variation affects some fitness parameters. Female fecundity increases with body size while energy per unit of female weight, allocated per egg, decreases (Honěk, 1986b, 1992). Variation of individual fitness, due to differences in body size, may be more important than the variation, due to different wing morph. Average body size in the open (Fig. 5) is determined by the prevailing weather during the late period of larval development. The annual variation in body size and fecundity is large. Within years female length is correlated loosely with potential fecundity (Honěk, 1986b).

Usually, the length of adult life varies from two months to a year, depending on whether the individuals are maintained under conditions favouring reproductive activity or diapause (Rizki & Sláma, 1968). However, it was found that approximately 20% of adult males can live nearly 2 years (Honěk, unpubl.) Matings may begin within a few days of adult life, under favourable temperature and photoperiod (Žďárek, 1968, 1971). Active adult females undergo distinct reproductive cycles, each terminated by oviposition of about 40–80 eggs. Eggs mature and are oviposited without respect to insemination. The first gonadotropic cycle takes about one week and, usually oviposition, starts on 7–10th day after adult emergence. Successive cycles become shorter in duration, lasting from 2 to several days, depending on temperature (Sláma, 1964a, 1965c; Rizki & Sláma, 1968; Socha et al., 1988, 1991). Exceptionally, the females were observed to scrape small hollows, lay eggs into them and then cover the latter (Seidel, 1924; Polozhencev & Polozhenceva-Korovina, 1961). In this case, *P. apterus* should be classified, not as a “subsocial” but, as a “praesocial” insect species, characterized by parental care of offspring.

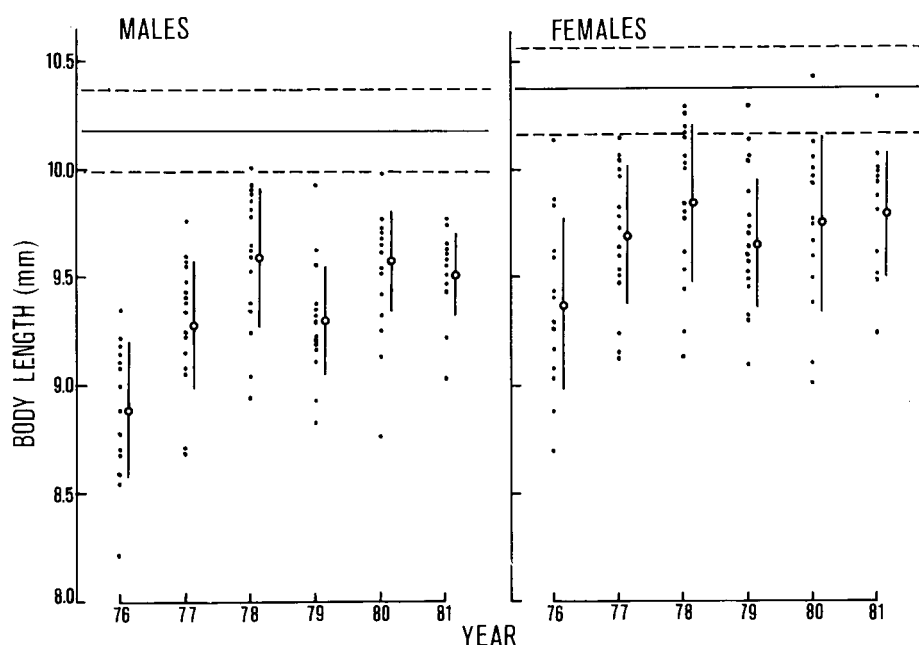


Fig. 5: Constraints on average body size in natural populations of Central Europe. Body length in 17 local populations of Bohemia (points) and mean ($\pm$ standard deviation) for all populations, in 1976–1981. Compared with average (solid line) body length $\pm$ standard deviation (ashed lines) of laboratory populations reared at optimum trophic conditions, under long-day photoperiod and 26°C. From Honěk (1981).

In Central Europe, the majority of bugs do not lay mature eggs in the same year as they become adults; they undergo a period of facultative diapause (Hodek, 1968, 1971a). During the late autumn, winter and early spring, the adults are mostly inactive in litter under old lime-trees. They may exhibit some movement, when warmed by sunshine. If there is snow cover, the bugs withstand temperatures falling in January and February to about -20°C . In the field, the resumption of development is delayed by low temperature (Hodek, 1971a). The overwintered females start to lay eggs in April or May, and most larvae hatching from eggs become adult in late summer (Hodek, 1968; Saunders, 1983). Diapause in this species can be induced artificially, prevented and terminated under laboratory conditions (Hodek, 1968).

The relationship between growth rate and long-day diapause incidence has been demonstrated (Hodek, 1968; Honěk, 1983). Unfavourable conditions such as pollution, over-crowding, isolation and starvation reduced considerably the rate of larval development. An increase in duration of larval development could thus be perceived to be a general symptom of adverse external conditions and might be a useful token stimulus for long-day diapause induction (Honěk, 1983). The mechanism which enables the insect to adjust diapause according to the growth rate of larvae may be of ecological significance.

Aggregation

Immature stages of *P. apterus* tend to form aggregates. The aggregate formation is not due to passive clustering around a food resource, but due to interindividual attraction guided by visual and chemical stimuli (Herter, 1924; Staddon & Daroogheh, 1982; Schmuck, 1987). Several abiotic factors such as temperature, air humidity and moisture content of the substrate affect the aggregation tendency, as well as the diurnal rhythm of the bugs and their changing ecological requirements (Herter, 1924; Schmuck, 1987). Contact pheromones play an important role in formation and maintenance of aggregations (Schmuck, 1987). The perception of the identification marker takes place via the last antennal segment, a region rich in receptors called "sensillae styloconicae" (Žďárek, 1970). The functional properties of abdominal trichobothria (that transmit the signal) and excitation dynamic in the bug were studied by Drašlar (1973) and Gaffal (1971).

The larvae possess three dorsoabdominal glands (DAG) (abdominal terga 3,4 5). The small anterior (DAG 1) and median (DAG 2) glands are still functional in adults, whereas the posterior defensive gland (DAG 3) is active in the larvae only (Farine, 1989). A striking difference in both the histology and secretory organelles of the third and the second gland have long been known (Mayer, 1874; Stein, 1966a,b, 1967; Schumacher, 1971a,b). Paired metathoracic glands, opening at the base of the hind legs, are observed in adults of both sexes and a sternal glandular epithelium (sterna 2–6) occurs in males only (Farine, 1989; Farine et al., 1992). In larvae, the aggregation pheromones are produced, at least in part, in the dorsoabdominal gland, whose secretion contains the n-alkanes, n-tridecane to n-hexadecane and n-heneicosane (Schmuck, 1987).

The third dorsoabdominal gland contains components typical for defensive secretion, secretions which are also found in the metathoracic defense glands of the adults (Schmuck, 1987). The chemicals produced deter predators (e.g., ants), elicit an alarm response for only a very short time, and induce the dispersion of the bugs (Schmuck, 1987; Farine, 1989). The exocrine secretion may also be considered as defensive, the ants not only being repelled but also paralyzed (Farine, 1989). In a more detailed study of the defense-secretion, 2 of the 3 compounds were identified as (E)-2-octenal and 4-oxo-(E)-2-octenal (Staddon & Daroogheh, 1982). The defensive secretions from larvae and adults of both sexes were recently investigated chemically by Farine et al. (1992, 1993). Forty components were identified from the larval posterior dorsoabdominal glands and 35 from the adult metathoracic glands. Within 43 identified chemicals the authors found 23 aldehydes, five saturated hydrocarbons, five alcohols, three ketones, three lactones, two terpenes, one phenol and one ester. Whereas eight components are specific to the larvae, methyl pentenal, (E)-2-hexenol, and heptadecanal are the only adult-specific components. The exact biological role of all identified chemicals is almost unknown (Farine et al., 1992); many of them are considered to have a defensive function.

Host plant preference

Basic spectrum of host plants shared by all pyrrhocorids is represented by the order Malvales (Malvaceae, Tiliaceae, Bombacaceae and Sterculiaceae). The pyrrhocorids have adapted themselves to the extremely dry diet of ripe seeds. They are conspicuously polyphagous and, consequently, tend to colonize some unrelated plants (Stichel, 1959; Tischler, 1959; Doesburg 1968; Puchkov, 1974; Ahmad & Schaefer, 1987). According to

Ahmad & Schaefer's (1987) critical review, it is possible to point out that there are several exceptions from the above rule: *Roscius* and *Melamphus* seem to be adapted to feed on Flacourtiaceae and Kiggeleriaceae (Violales); *Pyrrhocoris* and *Scantius* seem to be more polyphagous than other pyrrhocorid genera; *Antilochus* and *Dindymus* are predominantly predaceous.

P. apterus is feeding, mainly, on seeds of linden trees (*Tilia cordata* Miller or *T. platyphylos* Scopoli) or plants such as mallows (Malvaceae) (Tischler, 1959; Polozhencev & Polozhenceva-Korovina, 1961) and other plant species (Lipowa & Lipa, 1957; Stichel, 1959; Tischler, 1959; Puchkov, 1974). In Central Europe, *P. apterus* clusters, often in large numbers at the feet of linden trees, whose seeds form the basic component of its food. Southern populations of *P. apterus* (from Israel) can adapt easily to new kinds of food (e.g., from mallows to linden seeds) (Socha, unpubl.). The bug has been reported as being carnivorous occasionally (Southwood & Leston, 1959) and feeding on dead animals (for literature see Puchkov, 1974). Henrici (1938) was able to rear this species on pieces of the larvae of *Tenebrio*. In addition, the bug is also known to attack weakened or freshly moulted individuals of its own kind. Polyphagy is one of the main reasons for the widespread occurrence of this species and its subsequent expansion to India and America.

Since this species may be reared easily on dry linden seed and water in the laboratory (Sláma, 1964a,b; Hodek, 1968, 1971a,c), it serves as a convenient material for experimental studies.

LIFE CYCLE STRATEGIES

Diapause and cold hardiness

Diapause of *P. apterus* adults is characterized by an arrest of reproduction (Sláma, 1964a; Hodek, 1968); the ovaries of diapausing females are inhibited in the previtellogenic stage (Fig. 6). Adult diapause is controlled by photoperiod (Hodek, 1968, 1971a, 1983; Hodková et al., 1991) on the basis of humoral and nervous regulation of the CA (Sláma, 1964a; Žďárek, 1968; Hodková, 1976, 1977a, 1979). While short days (12L : 12D) induce diapause, long days (18L : 6D) prevent and terminate it; the response concerns the entire population (Hodek, 1968). However photoperiodic termination does not seem to occur in Central Europe. Diapause can also be induced in 85–90% individuals even under long days by a short (2–4 days) decrease to low temperatures above zero (Hodek, 1971b) or by very high population density (700 individuals in 4000 ccm) in 40% (Hodek, 1968). The incidence of long-day diapause is correlated positively with retardation of growth in the last larval instar (Honěk, 1983).

Adult diapause of the bug can be pre-programmed in the larvae by short-day photoperiod action, from the beginning of the 5th larval instar (Hodek, 1971c) or, perhaps, earlier (Saunders, 1983). Photoperiodic summation is temperature-dependent in *P. apterus* (Hodková & Hodek, 1987, 1989). The larvae are able, for at least the last 12 days before adult ecdysis, to register, store and pass over to the resulting adults the diapause preventing signal (Hodek, 1971c) (Fig. 7). If the adults do not enter diapause, they remain sensitive to photoperiodic induction for their entire life (Hodek, 1968). The same is true if they are activated from diapause by diapause preventing photoperiod (i.e., by tachytelic processes). Thus diapause can be terminated and reinduced several times during adult life (Hodek, 1968; Goryshin & Volkovich, 1978; Hodek & Hodková, 1986). In contrast, the

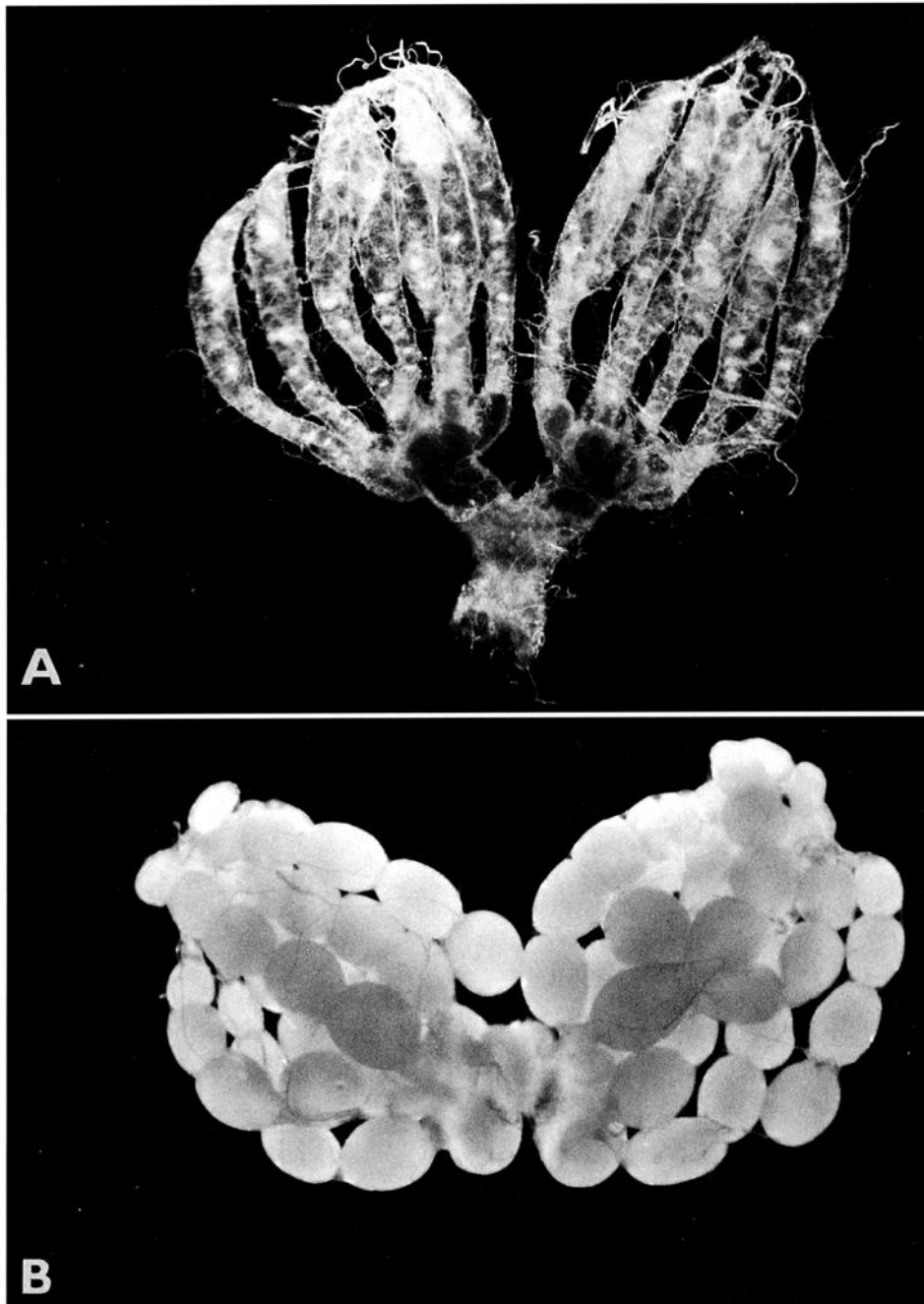


Fig. 6: Ovaries in diapausing (A) and reproducing (B) adult females of *P. apterus*. The ovaries of diapausing female are arrested in the previtellogenic stage; ovaries of reproducing female are in the stage of choriogenesis.

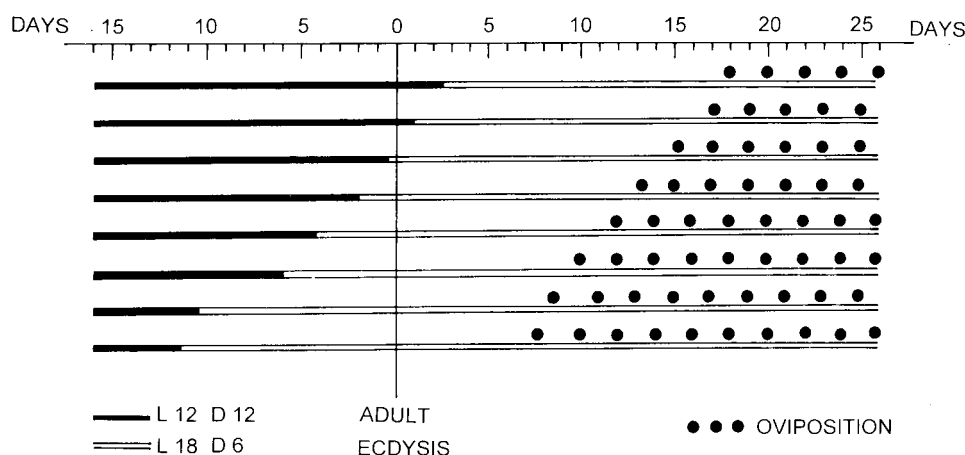


Fig. 7: Effect of larval treatment with a long-day photophase on average duration of pre-oviposition period (single pairs of *P. apterus*). From Hodek (1971c).

photoperiodic response is lost irreversibly by the completion of diapause development, by horotelic processes (Hodek, 1983). Therefore, post-diapause adults can oviposit in spring when the photoperiod is still below the critical length. The photoperiodic activation at 18L : 6D can be inhibited by low temperature of 15°C (Hodek & Hodková, 1986).

Diapause intensity decreases gradually with time. This process can be monitored by transfers of bugs from their dormancy sites to 25°C and contrasting photoperiods. At long days (18L : 6D), the progress and completion of diapause development was indicated by shortening of oviposition delay (pre-oviposition period) (Fig. 8A). From about 30 days in August and September this delay decreased to 8–9 days in January, i.e., to the duration of pre-oviposition period of normally reproducing females. Transfers to short days (12L : 12D) revealed a gradual loss of photoperiodic response in the population (Fig. 8B). While in August and September the oviposition was averted in all females, in October 10–30% of females lost their photoperiodic response, and in December all (or almost all) females oviposited (Hodek, 1971a, 1974, 1988; Socha & Šula, 1992). Thus, in Central Europe, natural daylengths induce diapause after early August (Hodek, 1971a; Honěk & Šrámková, 1976; Socha & Šula, 1992) and the diapause ends in December, i.e., before the advent of hard frost. Bugs then spend the rest of cold season in a state of post-diapause quiescence (Hodek, 1971a; Socha & Šula, 1992). Post-diapause vitellogenesis can be prevented by starvation (Hodková, 1982). Since vitellogenesis is prevented in starving females, diapause completion can be separated reliably from the post-diapause morphogenesis (Hodek & Hodková, 1986).

Two different critical daylengths inducing diapause were reported in this species for bugs from central Bohemia (50°N, 430 m): 17L : 7D by Hodek (1968) and 15.75L : 8.25D by Saunders (1983). A lower critical daylength (15L : 9D) was found in bugs from Yerevan, Armenia (40°N, about 800 m) (Volkovich & Goryshin, 1978). A diapause induction-termination asymmetry in photoperiodic responses was reported for this bug by Saunders (1983). The photoperiodic reactions under light-dark cycles of various duration (Goryshin & Tyshchenko, 1976) and the influence of constant and gradually increasing

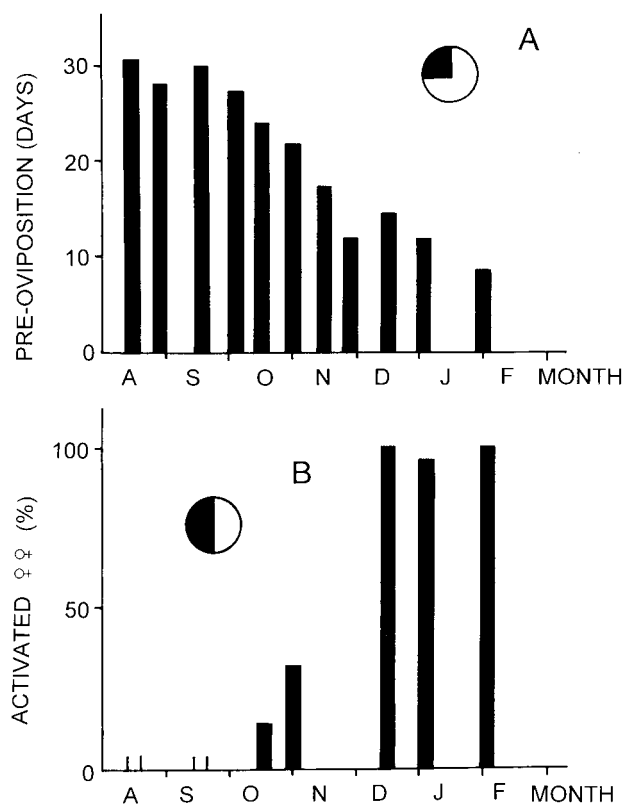


Fig. 8: Activation of bugs collected at Slaný 1967–68 under long-day (A) and short-day (B) photoperiods. From Hodek (1971a).

photoperiods on induction of reproductive activity (Volkovich & Goryshin, 1979) were also studied. Two main factors were shown to determine the photoperiodic reaction at the constant photoperiods: critical daylength and critical number of long days.

Laboratory exposures to constant temperatures proved that diapause development can be completed not only at 5°C, but also 15°C. However, the latter temperature decreased the fecundity of postdiapause females (Hodek, 1978). At low temperatures insects use few reserves and the vitality of dormant insects is thus conserved, or mortality prevented (Hodek & Hodková, 1988). Very high temperatures (mid-day max. 40–42°C), and particularly an increase in temperature, can stimulate a proportion of the females (e.g., 49%) to oviposit even at short days (Hodek, 1968).

Two characters, the diapause and the wing polymorphism, are controlled by photoperiod in *P. apterus*. In spite of the lack of morphoregulative effect of photoperiod, the selected macropterous strain of this species, like the wild-type brachypterous morphs, retained full capacity for diapause induction (Honěk, 1979). Nevertheless, the possibility of changing the photoperiodic reaction by selection, with respect to diapause, was also

demonstrated. Two strains from different geographical populations were selected for a *non-diapause* (*nd*) character under short-day (12L : 12D) photophase (Hodková & Socha, 1992; Socha & Hodková, 1994). The *nd* strain of *P. apterus* was established after 5 generations of selection. The *nd* bugs lost the photoperiodic response at $26 \pm 1^\circ\text{C}$ in all experimental photoperiods tested, including the continuous darkness. Reciprocal crosses between *nd* and wild-type bugs demonstrated an autosomal recessive behaviour of the *nd* trait in the short-day photoperiods, but its autosomal dominant behaviour in continuous darkness. It was found that photoperiodic response in the *nd* bugs is not expressed at 26°C . However, recent experiments (Hodková and Socha, in prep.) demonstrated that the photoperiodic clocks were not removed by selection in the *nd* strain, because they can be expressed easily at lower temperatures ($16\text{--}19^\circ\text{C}$), either in constant or thermoperiodical application. No substantial difference in diapause intensity between different geographic populations was observed (Volkovich & Goryshin, 1978); but new results show that such a conclusion cannot be generalized (Socha, unpubl.).

Sláma (1964a,d) reports a steep increase in metabolic rate at the end of diapause. Only a slight increase was found when the bugs were kept at a moderate temperature of 15°C which is suitable for diapause development but prevents oviposition. The steep increase in O_2 consumption thus appears to be connected rather with the onset of morphogenesis than with diapause termination (Hodek & Hodková, 1981).

The diapause of both males and females of *P. apterus* is attended by the synthesis and accumulation of particular storage proteins (SP_1 and SP_2) (Socha et al., 1991; Socha & Šula, 1992). The SPs occur not only in diapausing adult bugs, but also in control last instar larvae and reproductive adults, even though at much lower titres (Socha et al., 1991). The SPs in the haemolymph are subunits of a larger storage protein and their synthesis depends upon the absence of JH (Socha et al., 1991). They may provide a source of amino acids during diapause and especially after its completion.

The patterns of the SPs are related to the developmental stage of the ovaries (Socha & Šula, 1992). High haemolymph amounts of SP_2 were typical for adults in September, October and November. No differences in the haemolymph protein patterns were noted between adults in diapause (September–November) and post-diapause (January–February). Although the January and February adults were no longer sensitive to the short-day photoperiod they retained the same haemolymph protein pattern as diapausing adults, which had not yet lost their sensitivity. The female protein pattern, which is typical of this spring season (March and April), was characterized by simultaneous coincidence of high titres of SP_1 , SP_2 and Vg. The SPs appear to be synthesized in autumn and persist in the haemolymph until spring (Socha & Šula, 1992). It indicates that their occurrence is not confined to the diapause syndrome in this species. Likewise, the diapause completion in *P. apterus* is not connected directly with the loss of cold tolerance (Hodek, 1971a; Hanzal, 1988), there is no close relation between the occurrence of the SPs and the effects of cold and diapause (Socha & Šula, 1992). The same is valid for the low-molecular weight proteins (about 16 and 18 kDa) reported by Hanzal (1988) as “cold proteins”. The latest results (Socha & Šula, unpubl.) indicate that 16 and 18 kDa polypeptides do not represent typical “cold proteins”, because they also occur in adults reared in the laboratory under short day conditions at a constant temperature of 26°C and their titres increase only with the duration of diapause. Apparently, cold can accelerate their accumulation only.

In addition to the inhibition of morphogenesis, photoperiodic induction of diapause seems to be a prerequisite for the increase in cold hardiness in *P. apterus* at high temperature (Hodková & Hodek, in prep.). Both effects are mediated by inactivation of the retrocerebral complex. The absence of hormones enables further decreases in the supercooling point by cold acclimation. The lowest supercooling point was recorded in *P. apterus* in the field in late January and early February, i.e., at a time when diapause was over. Therefore it is assumed that the decrease of supercooling point by cold acclimation and the maintenance of cold hardiness are made possible by the traits persisting from diapause syndrome rather than by diapause inhibition itself (Hodek, 1971a; Hodková et al., 1992; Hodková & Hodek, in prep.).

Voltinism

Diapause of *P. apterus* is facultative and all individuals from the Czech localities studied are potentially polyvoltine (Hodek, 1968). Under natural conditions their voltinism depends on seasonal changes of temperature and photoperiod. Hodek (1968, 1971a) reported a univoltine cycle for localities in northern and central Bohemia and the years 1964–68.

In warmer years and places a partial second generation might develop theoretically (Honěk & Šrámková, 1976); however, it is considered as a rather unfavourable modification of the life cycle due to total mortality of the 2nd generation larvae and lower survival of their parents. According to these authors, an existence of the 2nd generation could disrupt the life cycle of *P. apterus*. In order to ensure the monovoltine cycle of this species in climatic conditions of Central Europe (Saunders, 1983; Honěk, 1986c), even during the warm years, an active behavioural selection of the microclimate is proposed (Honěk & Šrámková, 1976). The speed of *P. apterus* development is supposed to be regulated by the control of body temperature through an active selection of microhabitats with temperatures which do not exceed 24°C.

However, recent results (Socha & Šula, 1992, in press) indicate that the occurrence of two generations of *P. apterus* within one year is not an unusual phenomenon in Czech Republic [e.g., in České Budějovice (southern Bohemia), 49°N], but that it depends on temperature. A second generation arises from eggs laid by females emerging between June and the beginning of August. Socha & Šula (1992) found that almost 40% of July reproducing females contained mature eggs in their ovaries but no corpus luteum. This fact excludes the possibility that these females could be overwintering. In these females oviposition takes place, before diapause is induced by the shortening of the photophase in late summer. Adults that emerged later enter diapause without having laid eggs. These and the latest results (Socha & Šula, unpubl.), showing a considerable percentage of the second generation larvae to be able to mature into adults in the same year, prove that a portion of the Czech populations of *P. apterus* can found a second generation in warmer years and places.

Wing polymorphism, its control, and migration

Wing polymorphism is common in Heteroptera (Andersen, 1982; Puchkova, 1971; Roff, 1986). Two or more distinct morphs, long-winged (macropterous) and one or more short-winged (meiopterous = brachypterous, micropterous, apterous, etc.), usually occur,

and they often differ from each other in a variety of physiological and behavioural traits in addition to wing length (Roff, 1986).

P. apterus is characterized by the high morphological and developmental plasticity of the wings (Fig. 9). Based on analysis of wild populations, the bug is described as a dimorphic species producing brachypterous and macropterous morphs (La Greca, 1949; Seidenstücker, 1953; Tischler, 1959; Honěk, 1976a,b, 1981). The standard, brachypterous morph (Fig. 9A) is characterized by reduced forewing membranes and by hindwings atrophied to rudimentary scales. In macropters (Fig. 9B), both fore- and hindwings reach, or even exceed, the abdominal tip and the forewing membranes are usually well developed (Seidenstücker, 1953; Honěk, 1976a,b). Since the forewings of macropters overlap, resting individuals have either the right or the left wing uppermost and display an asymmetry in the forewing position (Ludwig, 1931). According to the wing ratio, asymmetry of the forewing position in *P. apterus* is of a dextrally amphidromic type (Škapec & Štys, 1980).

Collection of several strains and mutations of *P. apterus* (Socha, 1984, 1987a,b, 1988a,b) made it possible to complete detailed studies on morphological and genetic aspects of wing pattern determination. A morphometric analysis of wing length pattern in relation to genetics was also studied (Socha et al., 1993). Developmental trajectories leading to either brachypterous or macropterous morphs are genetically determined but environment-dependent. The macropterous form is inherited as a single recessive. Penetrance of the macropterous morph is determined by polygenic modifiers with interaction (Honěk, 1986a). Intensive selection against these modifiers produced a strain yielding a high proportion of macropters under any photoperiodic conditions (Honěk, 1979). The effect of modifiers depends on environment conditions. Long photoperiod and high temperature encourage production of macropters, while short photoperiod, a brief exposure to cold (Fig. 10) (particularly in early 5th instar), and rearing of larvae under isolation favour production of brachypters (Honěk, 1974, 1976b, 1981). The effect of long-day photoperiod may be transmitted through eggs to the next generation and become manifest under short day conditions promoting production of brachypters (Honěk, 1980). In the open the proportion of macropters varies annually due to variation in average temperature during larval development, so that high temperature increases the proportion of larvae which develop to adults under macropter-promoting long-day photoperiod. In Central Europe, individuals which moult to adults before late July become largely macropters. The rest of population moulting later on become brachypters. As in Central Europe most individuals moult in August and early September, natural populations are chiefly brachypterous (Honěk, 1981).

There was little genetic variations in tendency for macropterism among Central European, Mediterranean (Sicily and Eastern Turkey) and Central Asian (Kazakhstan) populations (Honěk, 1987a). Contrary selective pressures may ballance the tendency for macropterism. The only ecophysiological difference between adults of macro- and brachypterous morph is a longer pre-oviposition period in the former (Fig. 11) and significantly greater diapause incidence in early summer (Honěk, 1985). Being a macropter may then bring some advantage, since diapause prevents the immediate reproductive activity and establishment of a second generation, endangered by the approaching end of the season (Honěk, 1985; Honěk & Šrámková, 1976). This selective advantage of the macropters is perhaps the cause of a persistence of low level of macropterism in wild populations of *P. apterus*. Recessive macropterous homozygotes have longer development than the

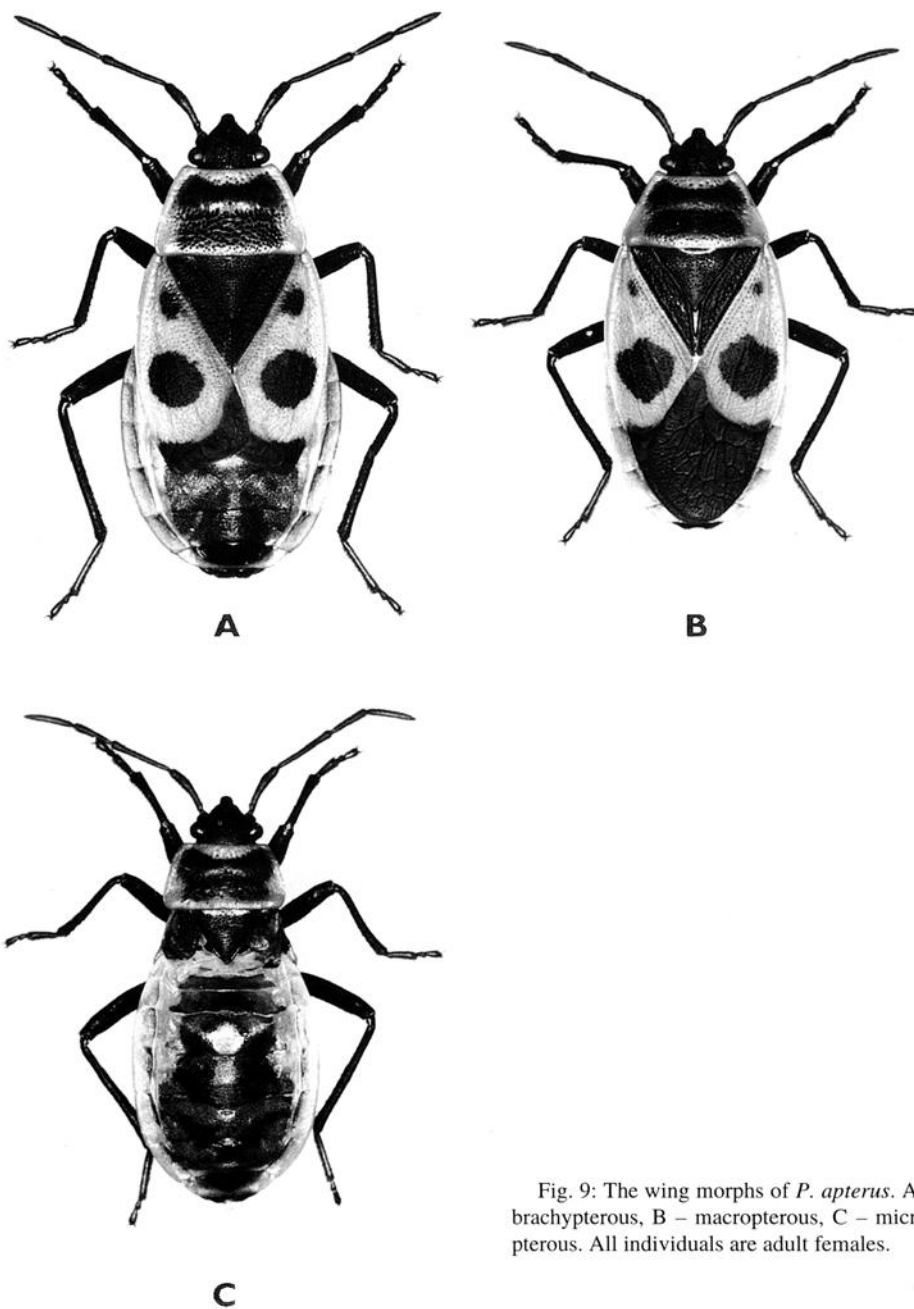


Fig. 9: The wing morphs of *P. apterus*. A – brachypterous, B – macropterous, C – micropterous. All individuals are adult females.

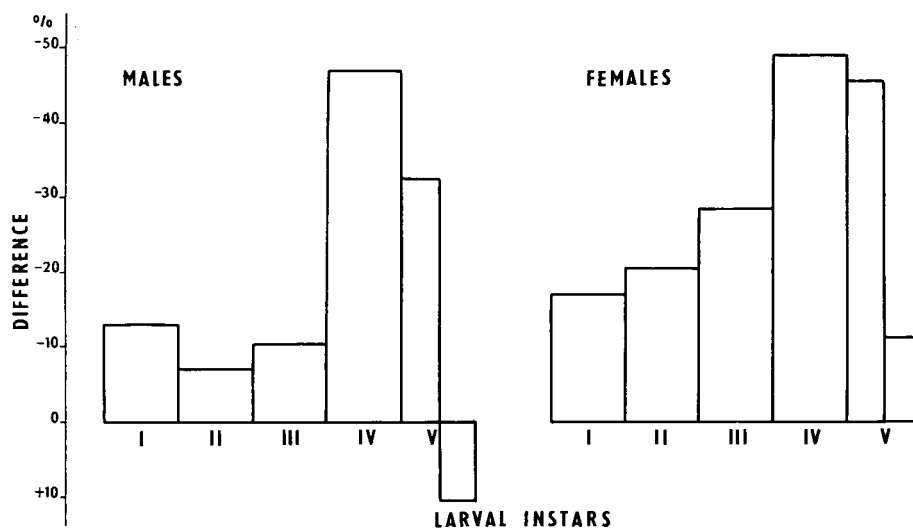


Fig. 10: Decrease in production of macropters following a brief cold treatment during larval development. Difference in the percentage of macropters against control (zero level) after a 2 day exposure of different larval instars to 8°C. From Honěk (1981).

dominant brachypterous homozygotes and may be brachypterized secondarily by effects of low temperature in the late larval stage. The genetic tendency for macropterism may thus increase the developmental time. A selection may exist against such individuals which may be killed by frost late in the season (Honěk, 1987a). Geographic differences in distribution of macropters between local populations are not thought to be related to different migration strategies (Honěk, 1981, 1985, 1987a). Such an explanation cannot be generalized apriori, because macropters in some wild populations of *P. apterus* were reported to fly (Seidenstücker, 1953); however, the flying ability of this bug was not observed by other authors. Nevertheless, some macropterous adults segregated in the selected *ma* strain of *P. apterus* was observed to move and raise both wing pairs (Sláma, Honěk, Socha, unpubl.).

Micropterism is somewhat rare in wild populations of *P. apterus* regardless of their geographical distribution. Nevertheless, an occurrence of micropters (Fig. 9C) or asymmetric individuals in wild populations of *P. apterus* was reported (Müller, 1926; Lang, 1946; Balazuc, 1951; Seidenstücker, 1953; Stehlík, 1954) and even described as f. *inaequalis* (Stichel, 1959). A very high frequency of micropters, often with asymmetric wing pairs, was found in the *ump* strain (Socha et al., 1993). In micropters, both fore- and hindwings are reduced considerably. The distal margins of the forewings are irregularly developed and, usually, the hindwings are atrophied to small scales, as seen in the brachypterous wing morph.

It appears that the unstable wing micropterism is linked with colour mosaicism (Socha, 1987a). The micropters, both symmetric and asymmetric, appear predominant among the *ump* individuals of the mosaic phenotype category (i.e., among those with mosaic

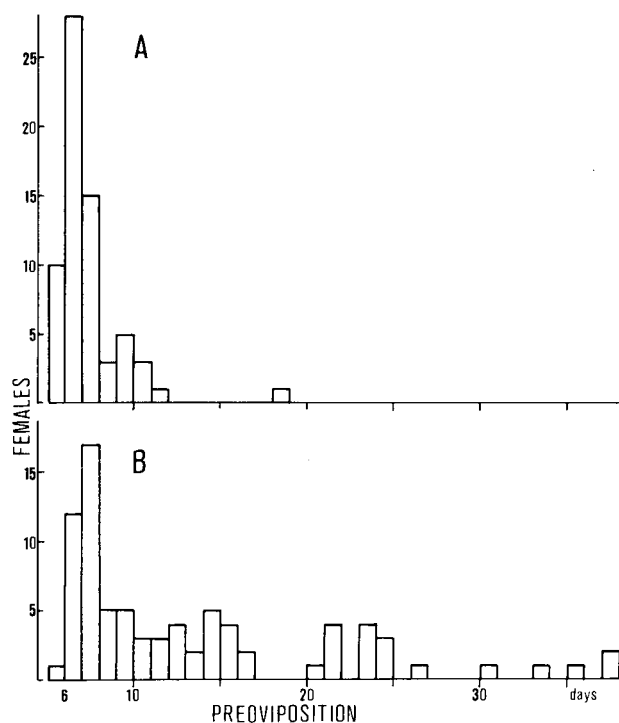


Fig. 11: Length of pre-oviposition period in 66 brachypterous (above) and 81 macropterous females (below) reared from eggs in long day conditions and 26°C. The ordinate indicates number of females starting the oviposition each day. From Honěk (1985).

colouration of the epidermis); they are very rare in the bugs of wild-type phenotype category. While the stable wing morphism of some heteropteran species was shown to be inherited as a simple Mendelian character or in a polygenic manner (Roff, 1986), no explanation for determination of unstable wing morphism has yet been described. The wing alone is subjected to this developmental mechanism, and not the animal as a whole. Explanations of this phenomenon, based upon trauma or infection are unacceptable, taking into account the high frequency of the bugs possessing unstable wing pattern, regularly segregated in each generation of the *ump* strain (Socha et al., 1993). It indicates some extraordinary genetic (and/or epigenetic) mechanisms involved in determination of this trait that lead to uncoupled development of the individual wings. Predominant segregation of micropters within the mosaic phenotypic category of *ump* strain indicates the close linkage of genetic factors determining both the *mo* and *ump* traits. This presumption is also supported by the results of reciprocal crosses between *ump_{mo}* micropters and wild-type bugs. The crosses show a similar genetic nature for the *mo* and *ump* strains; both are genetically unstable and inherited as sex-linked recessives (Socha, 1987a, in prep.). The *mo*

mutation of *P. apterus* is possibly transposon-mediated. The *ump* mutant strain (a sub-strain of *mo*) displays a similar behaviour, is unstable, and exhibits the same mode of X-chromosome-linked inheritance (Socha, 1987a; Socha et al., 1993). Thus, inheritance of the wing length in the *ump* strain can also be based on transpositions of mobile genetic elements. An unstable mosaicism in wing length pattern could be the first case of a mobile genetic element-controlled character, outside of the Holometabola.

It is presumed that such an *ump*-like genetic mechanism (but not linked with colour mosaicism) is also distributed within wild populations. Naturally, such a mechanism should be expected to occur with higher frequency among non-flying pterygopolymorphic species, like *P. apterus*, because there is no selective pressure on wing development that would support stable macropterism (Andersen, 1982). A high level of micropterism in the *ump* strain of *P. apterus* suggests that this wing morph represents a cryptic developmental potential of the species, and, perhaps, also one of the possible general trends in wing pattern evolution of Pyrrhocoridae.

PATHOGENS, PARASITES, SYMBIOTES AND PREDATORS

In Pyrrhocoridae there are no conspicuous organs like the rows of gastric caeca which contain large numbers of symbiotic bacteria.

The bacterial flora of the intestinal tract of *P. apterus* was examined, in histological sections and smears, by Kuskop in 1924 (in Haas & König, 1987). However, the isolation and characterization of aerobic and anaerobic bacterial flora from the mid-gut of this species was performed much later (Haas & König, 1987). A Gram-positive anaerobic bacterium, sharing some characteristics with the genus *Bifidobacterium*, was the first anaerobic microorganism isolated regularly from the mid-gut of all stages, except the egg. However, the correct systematic position of this symbiot of *P. apterus* has to be determined. The bacteria have the task of decomposing the contents of the extremely dry diet of this seed-sucking pyrrhocorid (Haas & König, 1987).

According to Haas & König (1987) aerobic bacterial flora, associated with the posterior third of the midgut, include members of the genera *Streptococcus* and *Hafnia*, but these bacteria do not have a symbiotic function, as they were not found in all stages of *P. apterus*.

Leptomonas pyrrhocoris Zotta is the only known kinetoplastid flagellate found in *P. apterus* (Zotta, 1926; Lipa, 1963).

A microsporidian, *Nosema pyrrhocoridis*, was first described as a parasite of the red firebug by Lipa (1977). This parasite infects mainly the midgut epithelium and the Malpighian tubules. Its spores can be discriminated easily from those of *N. apis* Zander, as observed in the gut of *P. apterus* by Grobov (1967). However, it is probable that the presence of the latter microsporidian may be explained by the feeding of the bugs on dead animals, especially by sucking the body of dead *Apis mellifera* L. (Lipa, 1977).

P. apterus is often parasitized by mermithid worms, e.g., *Hexamermis albicans* Siebold (Southwood & Leston, 1959; Polozhencev & Polozhenceva-Korovina, 1961), as well as by the fungus *Empusa dysderci* Viegae (Polozhencev & Polozhenceva-Korovina, 1961). The bug is parasitized by mites, especially from the family Laelaptidae (Polozhencev & Polozhenceva-Korovina, 1961). Another species of parasitic mite, most probably from the superfamily Phytoseioidea (Evans, 1963) was found in all stages under hemielytra of

brachypterous and macropterous individuals of *P. apterus* (Socha, unpubl.; Zacharda, pers. commun.).

Despite the defensive secretion and vivid warning colour of *P. apterus* it is eaten not only by some birds and amphibians (Ulrich, 1953), but also by some mammalian species, e.g., badger (*Eutamias sibiricus*). The bug is attacked by other heteropteran species, e.g., *Prostemma aeneicolle* Stein, *P. sanguineum* Rossi (Nabidae) and *Rhynocoris iracundus* Poda (Reduviidae) (Polozhencev & Polozhenceva-Korovina, 1961). Other observed insect predators of *P. apterus* are ants (Farine, 1989).

CONCLUDING REMARKS

There are a number of other areas of research on the red firebug which have interesting implications. The bugs have been used for testing of newly synthesized prospective insecticides and chemosterilants. Some of the newest studies are directed toward the problems of determination of metameric pattern, cold hardiness and biorhythms. Since the culture of *P. apterus* is easily maintained in the laboratory, it is probable that, for many years, this species will be used as a convenient experimental model insect for future studies of basic biological and entomological problems.

ACKNOWLEDGEMENTS. The author thanks Drs K. Sláma, I. Hodek, J. Zrzavý (Institute of Entomology, České Budějovice) and A. Honěk (Plant Research Institute, Praha) for reviewing the MS, substantial modification of chapters Diapause and cold-hardiness, Voltinism (by I. Hodek) and Wing polymorphism, its control, and migration (by A. Honěk), and for the supply of Figs. 6, 7 (I. Hodek) 5, 10 and 11 (A. Honěk). Research on the morphology, physiology and genetics of *P. apterus* was supported by grants Nos. 60708 and 60717 from Czech Academy of Sciences.

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Received February 5, 1993; accepted July 2, 1993